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A Phylogeny of the Flatbill and Tody-tyrant Assemblage of Tyrant Flycatchers

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ABSTRACT

A phylogeny is developed for those tyrant flycatchers known variously as "flatbills," "tody-tyrants," and "pygmy-tyrants." Historically these flycatchers have been assigned to three different subfamilies, but an argument is presented here for their monophyly based on shared derived states of the nasal septum, interorbital septum, and nest form. Putative relatives that do not share these

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derived states are excluded from this assemblage: *Ramphotrigon* and *Pseudotriccus.*

Two primary lineages in the assemblage are defined by the basic morphology of the syrinx. *Rhynchocyclus, Tolmomyias, Onychorhynchus,* and *Platyrinchus* have at least one complete, calcified ring around each bronchus. In a second lineage, *Todirostrum, Poecilotriccus, Hemitriccus* (including *Myiornis*), *Lophotriccus* (including *Atalotriccus*), and *Oncostoma* lack any such bronchial support, but share two syringeal character states that are unique within the family. *Poecilotriccus* is enlarged to encompass the "*sylvia* species group" formerly in *Todirostrum.*

Cnipodectes does not fit easily into either of the primary lineages and seems not to have any close relative within the assemblage.

RESUMEN

Se desarrolla una filogenia para aquellos tiránidos atrapamoscas conocidos como "pico-aplanado" (flatbills), "tody-tiránidos" (tody-tirants), y "tiránidos enanos" (pygmy tirants). Históricamente, estos atrapamoscas han sido asignados a tres diferentes subfamilias, pero aquí se presenta un argumento favoreciendo su monofilia, basado en caracteres derivados compartidos del septo nasal, septo interorbital, y forma del nido. Relativos putativos que no comparten estos caracteres derivados son excluídos de este conjunto: *Ramphotrigon* y *Pseudotriccus.*

Dos principales lineajes están definidos por la morfología básica de la siringe. *Rhynchocyclus, Tolmomyias, Onychorhynchus,* y *Platyrinchus* tienen al menos un anillo completo, calcificado alrededor de cada bronquio. En un segundo lineaje *Todirostrum, Poecilotriccus, Hemitriccus* (incluyendo *Myiornis*), *Lophotriccus* (incluyendo *Atalotriccus*), y *Oncostoma* carecen de cualquier soporte bronquial, pero comparten dos estadios de caracteres siringeales que son únicos entre la familia. *Poecilotriccus* es ampliado para abarcar el "grupo de especies *sylvia*," ubicado anteriormente en *Todirostrum.*

Cnipodectes no entra facilmente en ninguno de los lineajes principales y no parece tener ningún relativo próximo dentro del conjunto.

INTRODUCTION

The tyrant flycatchers (Tyrannidae) whose relationships are explored in this report include genera that have been known variously as "flatbills," "tody-tyrants," and "pygmy-tyrants," group vernaculars that aptly allude to their predominant external morphological characteristics: (1) their small size and (2) their relatively flat bills, which may be broad and swollen or narrower and spatulate in shape. Previous dependence upon external morphology has resulted in a long tradition of these genera being assigned to three different subfamilies (Sclater, 1888; Berlepsch, 1907; Hellmayr, 1927). In this report I present an argument for their monophyly, identify two primary lineages within the assemblage, and examine the probable genealogical relationships within these lineages. I do not make judgments about species' limits, but instead follow Traylor (1979) in this regard.

Sclater (1888) placed the flatbills in his Elaineinae, *Onychorhynchus* and *Cnipodectes* in his Tyranninae, and *Platyrinchus* and the tody-tyrants in his Platyrhynchinae. Berlepsch (1907) had these taxa distributed among three different subfamilies, but brought them closer together sequentially: *Onychorhynchus* at the end of his Myiarchinae, the flatbills (including *Cnipodectes*) in a new subfamily Rhynchocyclinae, followed immediately by *Platyrinchus* and the tody-tyrants in a third subfamily, the Platyrhynchinae. Hellmayr (1927) and Zimmer (MS) retained this sequence, involving three subfamilies, but moved *Platyrinchus* in with the flatbills.

The concept that the flatbills and tody-tyrants might in fact be more closely related to one another than implied by Sclater's Catalogue has its roots in the evolutionary significance that Ihering (1904) attached to the pendant, enclosed nest built by a small number of tyrant flycatchers. He recommended that Sclater's Platyrhynchinae be divided into two subfamilies according to nest form. Those listed as being closely related because of their sharing the pendant, enclosed type of nest were several species of tody-tyrants and flat-

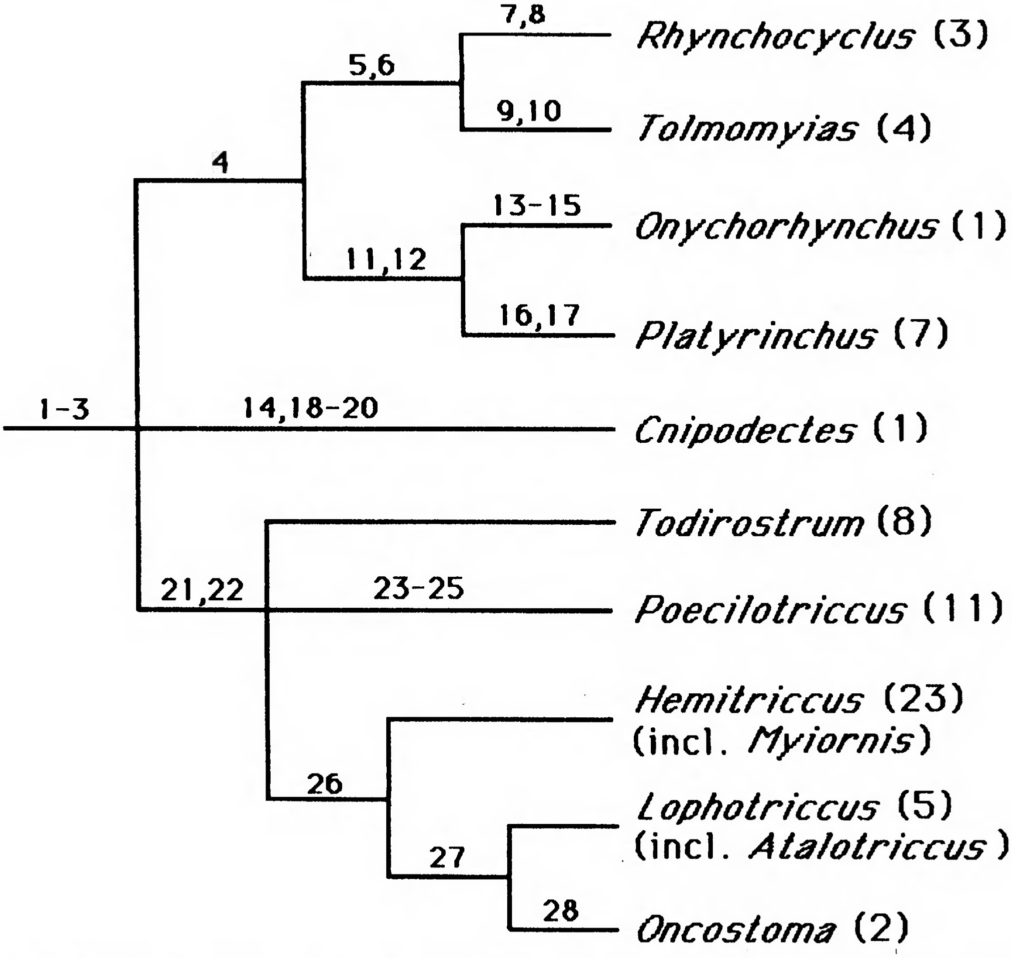

Fig. 1. Phylogenetic relationships within the flatbill and tody-tyrant assemblage (10 genera; 65 species). Letters identify diagnostic character states described in text and in table 1. Numbers in parentheses indicate number of species per genus.

bills, as well as *Platyrinchus* (though Ihering must have erred in the identification of this nest; see below).

Warter's (1965) study of the tyrannoid cranium provided the first substantial morphological evidence that *Onychorhynchus*, the flatbills, and the tody-tyrants might be more closely related than previously thought; he recommended that they be brought together into a single subfamily, but assigned them to separate tribes. Traylor (1977) placed the tody-tyrants and flatbills next to one another at the end of his enlarged Elaeniinae, but maintained *Onychorhynchus* apart, at the beginning of his Fluvicolinae.

METHODS

The methodology in this study is the same as that employed for developing phylogenies of other groups of tyrant flycatchers (Lanyon 1984, 1985, 1986, 1988a). Primary emphasis is placed on what I perceive to be shared derived character states of the cranium, the syrinx, and nest form, all of which are more conservative than the external morphological characters traditionally used to cluster genera in the Tyrannidae. As character states are identified and used to establish monophyly of the assemblage, a genus, or a cluster of genera, these character states are assigned

Table 1

Characters used for Phylogeny of the Flatbills and Tody-tyrants

	Character, description	Distribution by taxa
1	Nasal septum poorly ossified; typically a shallow remnant dorsally, with no transverse trabecular plate	All flatbills and tody-tyrants
2	Infraorbital fenestra much enlarged and supraorbital fenestra completely obliterated or nearly so	All flatbills and tody-tyrants except *Onychorhynchus*
3	Nest pendant, fully enclosed, with side entrance	All flatbills and tody-tyrants except *Platyrinchus*
4	At least one A element forms a complete, calcified ring around each bronchus	*Rhynchocyclus, Tolmomyias, Onychorhynchus,* and *Platyrinchus*
5	Internal cartilages narrow and basically linear in shape	*Rhynchocyclus* and *Tolmomyias*
6	Nest retort-shaped, with entrance at end of downward pointing tube or spout	As above
7	Internal cartilages are free within the tympaniform membrane, close to dorsal ends of the A1s but extending well beyond those elements	*Rhynchocyclus*
8	Cartilaginous ventromedial ends of the A1s broad and blunt	*Rhynchocyclus*
9	Internal cartilages attached to dorsomedial segments of the A2s, further from dorsal ends of the A1s and do not extend appreciably beyond the A1s	*Tolmomyias*
10	Cartilaginous ventromedial ends of the A1s are more delicate and curvilinear in shape	*Tolmomyias*
11	Internal cartilages very broad, shaped like a spatula or a child's mitten, with dorsal edge somewhat thickened to accommodate the "thumb"	*Onychorhynchus* and *Platyrinchus*
12	B1s very broad in their central regions	As above
13	Interorbital septum fully ossified, with interorbital fenestra obliterated	*Onychorhynchus*
14	Nest 2 to 6 ft long	*Onychorhynchus* and *Cnipodectes*
15	Intrinsic syringeal muscles lacking	*Onychorhynchus*
16	Broad internal cartilages partly ossified and connected to dorsal ends of A1s and A2s and to medial segments of A3s	*Platyrinchus*
17	B2s forked ventrally	As above
18	Internal cartilages forked distally and attached to dorsal ends of A3s	*Cnipodectes*
19	B2s slightly forked dorsally	As above
20	Male with outer primaries arcuate and all primaries more or less twisted	As above
21	Horseshoe- or V-shaped cartilaginous plate that interconnects the dorsal ends of the ossified A elements in each bronchus and the pessulus	All tody-tyrants
22	Delicate, slender, rodlike internal cartilages located near the caudal ends of the "horseshoe"	All tody-tyrants
23	Bronchial component of syrinx is longer and bowed or arched laterally	*Poecilotriccus*
24	Greatly enlarged and conspicuous plate of cartilage connecting the ventral ends of A1 through A4 elements	*Poecilotriccus*
25	Presence of rufous or cinnamon color in the plumage of various regions of the head	*Poecilotriccus*
26	Calcified pessulus extends anteriorly to divide four or more A elements dorsally	*Hemitriccus, Lophotriccus,* and *Oncostoma*
27	Conspicuous lateral compression of the trachea and tracheobronchial junction	*Lophotriccus* and *Oncostoma*
28	Calcified pessulus extends anteriorly to divide 19 or more A elements dorsally	*Oncostoma*

numbers in the text that correspond to the numbers in the phylogenetic diagram in figure 1 and table 1.

In addition to the anatomical collections at the American Museum of Natural History (AMNH), New York, I borrowed specimens from the Carnegie Museum of Natural History (CMNH), Pittsburgh; the Delaware Museum of Natural History (DMNH), Greenville; the Field Museum of Natural History (FMNH), Chicago; the Museu Parense Emilio Goeldi (MG), Belém, Brazil; the Museum of Natural History at the University of Kansas (UK), Lawrence; the Museum of Zoology at Louisiana State University (LSU), Baton Rouge; the Museum of Zoology at the University of Michigan (UMMZ), Ann Arbor; the National Museum of Natural History, Smithsonian Institution (USNM), Washington, D.C.; the Peabody Museum of Natural History at Yale University (PMNH), New Haven; and the collection of Peter L. Ames (PA). Specimens cited in the text, in figure captions, and in the Appendix are identified to collection by the abbreviations given above.

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MONOPHYLY OF THE ASSEMBLAGE

Nasal Capsule

Character states of the nasal capsule have been shown to be more conservative than external morphology, syringeal morphology, nesting behavior, and foraging behavior, and to have great value in identifying groups of tyrant flycatchers that have had a common ancestry (Lanyon, 1984, 1985, 1986, 1988a). It was perhaps understandable that the first of the tyrant flycatcher assemblages to be so identified and studied were those identified by the most obviously derived character states, and therefore those with well supported hypotheses of monophyly. In practice this translated into looking for character states unique to the group being studied. As happens with most character complexes, I soon reached that point in my ongoing analysis of tyrant flycatcher evolution where the differentiation between primitive and derived states of the nasal capsule became more difficult.

Warter (1965) and I (Lanyon, 1984) have suggested that the largely unossified state of the nasal capsule may be the primitive condition among tyrant flycatchers, since this is the state widely represented among suboscine families. Without a thorough study of the developmental patterns leading to the various ossified states, it becomes extremely difficult if not impossible, to recognize what may be legitimately derived states in those capsules that remain largely unossified. This was the dilemma that developed in my examination of the nasal capsule of the flatbills and tody-tyrants, which is poorly ossified.

The nasal septum is represented in cleaned museum skulls of flatbills and tody-tyrants only by a shallow ossified remnant dorsally (character 1). If the septum projects into the nasal cavity, its ventral edge is sharp and knifelike (as illustrated in most of the photographs in figs. 2–7), with no suggestion of a laterally projecting trabecular plate. Warter (1965) classified this simple septum as his "type 1" or "type 2." Often the dorsal remnant of the septum is strongly buttressed laterally, particularly at the base of what would have developed into the internal supporting rod had ossification proceeded as it has in other tyrant lineages; Warter labeled this the "type 3" nasal septum. In a few specimens of tody-tyrants, in which more of the septum has ossified, there may be a very narrow trabecular plate located somewhat above the ventral edge of the septum, creating the appearance of a sagittal ridge when viewed from below, but there is lack of consistency in this state, even within species. This unusual (for this assemblage) configuration of the septum is equivalent to Warter's "type 5," in which the plate is described as being "within the septum," and is the usual character state for those tyrant genera that I assign to the *Elaenia* assemblage (Lanyon, 1988a), where it is widespread and more fully developed. The size of this type of plate among the tody-tyrants varied from a mere suggestion of such a structure, as seen in *Poecilotriccus ruficeps* in figure 4: 7, 8, *Hemitriccus diops* in figure 5: 5, and in *Lophotriccus vitiosus* in figure 7: 3, 4, to a fairly well-developed plate seen in *Hemitriccus rufigularis* in figure 6: 1, 2.

The most conspicuous departure from the typical poorly ossified septum was found in three species of *Hemitriccus* (*margaritaceiventer, iohannis,* and *striaticollis*) and in *Atalotriccus pilaris.* Much of the ventral portion of the septum in these species is ossified and there is a broad trabecular plate along the ventral edge of the septum that tapers to a point posteriorly. The considerable breadth of these ventral plates can be appreciated best in the ventral aspects, as in figure 6: 6, 8 and figure 7: 6. This posteriorly projecting structure, being attached to and supported by the anteroventral portion of the septum alone, is vulnerable to breakage and loss, as indicated by the retention of an incomplete structure in figure 6: 3.

Due to extensive variation in the morphology of the nasal capsule described above, I could find no consistent differences that would serve as diagnostic characters at the generic level. Variation within species and genera often exceeded intergeneric variation.

Interorbital Septum

Warter (1965) reported that the flatbills and tody-tyrants have a "type 4" interorbital septum in which the infraorbital fenestra is much enlarged and the supraorbital fenestra is completely obliterated or nearly so (character 2). Working with a much larger data base (45 species instead of 22), I can confirm Warter's findings. With the exception of three genera (*Onychorhynchus, Rhynchocyclus,* and *Tolmomyias*) discussed in greater detail below, there is a remarkable uniformity within the assemblage with regard to the degree to which the supraorbital fenestra is obliterated by ossification of the dorsal most portion of the interorbital septum. Figures 8 and 9 illustrate intergeneric variation in this character within the flatbills and tody-tyrants, respectively. This configuration of the interorbital septum is also found in a number of other genera (*Phylloscartes, Pseudocolopteryx, Mionectes, Corythopis,* and *Pseudotriccus*) of small tyrants that I assign to my *Elaenia* assemblage (Lanyon, 1988a), where it is presumably convergent.

Nesting Behavior

The flatbills and tody-tyrants share a type of nest form (character 3) that is nearly unique among tyrant flycatchers and unquestionably derived. Nests are known for all 10 genera in the assemblage and, with the exception of *Platyrinchus,* all build pendant, fully enclosed nests with side entrances, often with a visorlike projection above (fig. 10). They have been variously described as pyriform, ovoid, or purse-shaped, and are nearly always suspended from the tip of a branch or vine (AMNH collection; Cherrie, 1890, 1916; Euler, 1900; Berlepsch and Hartert, 1902; Ihering, 1900, 1904; Carriker, 1910; Chubb, 1910; Todd and Carriker, 1922; Naumburg, 1930; Huber, 1932; Dickey and Van Rossem, 1938; Skutch, 1930, 1960, 1967, 1972, 1980; Snethlage, 1935; Griscom, 1932; Harrowes, 1936; Haverschmidt, 1950, 1965, 1968, 1974; Mitchell, 1957; Gilliard, 1958; Herklots, 1961; Smithe, 1966; Rowley, 1966, 1984; McNeil and Martinez, 1968; Wetmore, 1972; Gep, 1973; ffrench, 1976; Thurber, 1978; Traylor and Fitzpatrick, 1982; Hilty and Brown, 1986). According to Skutch (1960) this type of nest differs from other globular tyrannid nests in that it is formed by matting the materials together, rather than weaving them, and the nest chamber then formed by pushing the interior materials apart to create a cavity.

Ihering (1904) recognized the importance of nesting behavior in demonstrating relationships among tyrant flycatchers, and recommended a separate subfamily for those genera having a suspended, purse-shaped nest.

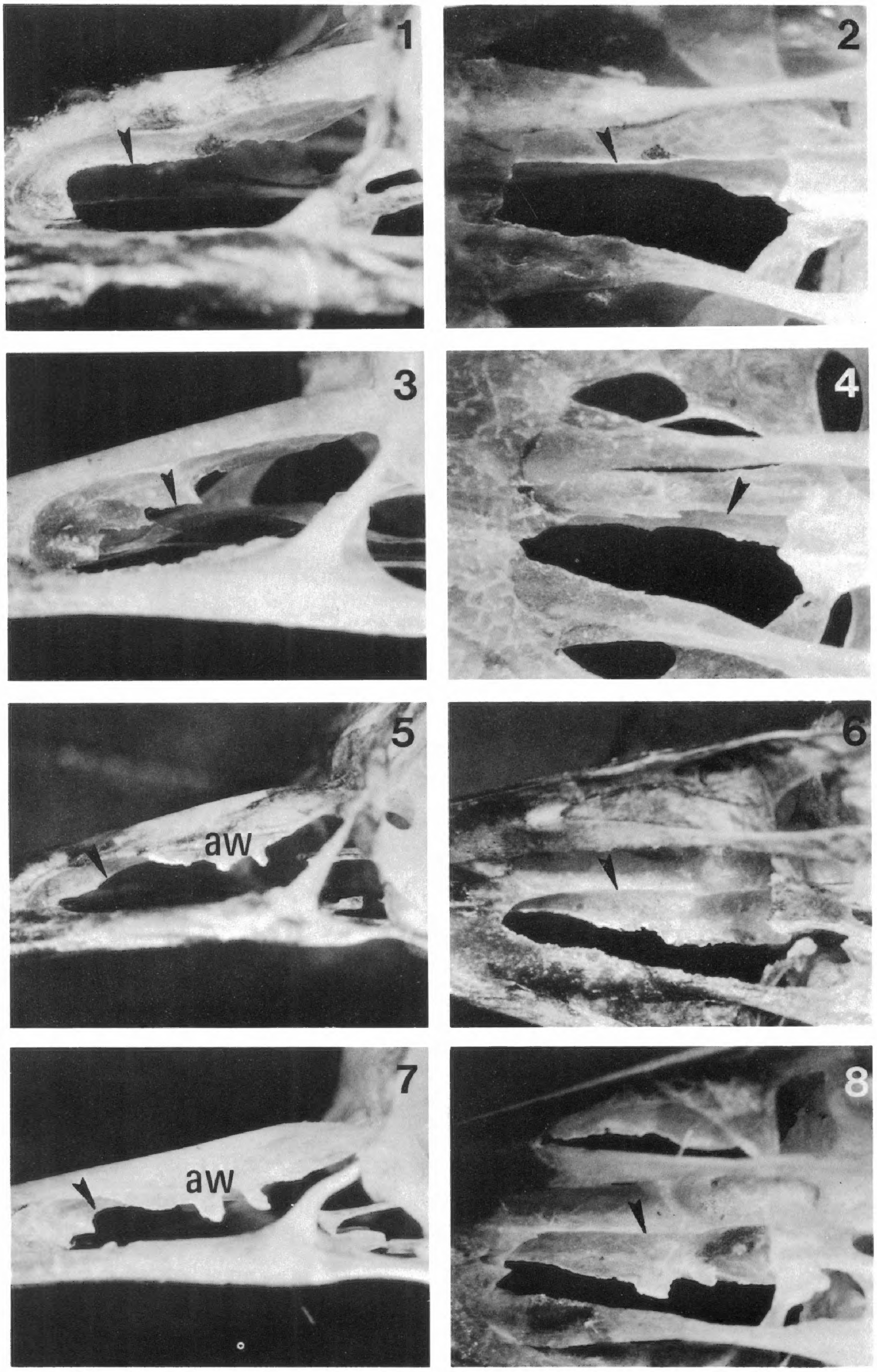

Fig. 2. The nasal capsule in *Rhynchocyclus* and *Tolmomyias* (anterior end of skull to left; skulls viewed laterally, 1, 3, 5, 7, and ventrally, 2, 4, 6, 8; magnification = 7×): **(1, 2)** *Rhynchocyclus olivaceus,* LSU 118512; **(3, 4)** *R. brevirostris,* AMNH 14478; **(5, 6)** *Tolmomyias poliocephalus,* FMNH 315990; **(7, 8)** *T. sulphurescens,* AMNH 10307. Arrows indicate knifelike ventral edge of nasal septum; **aw** = alinasal wall.

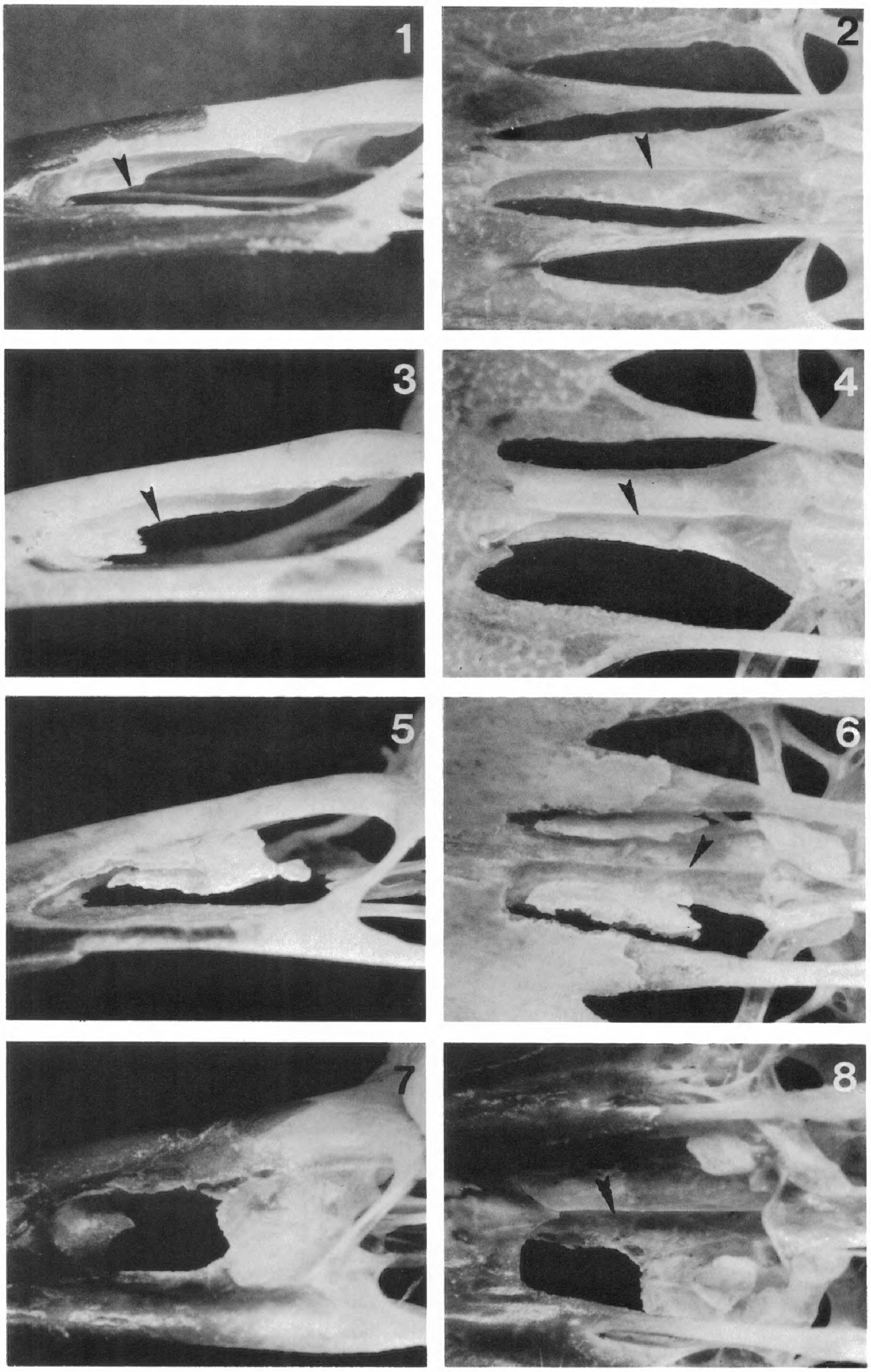

Fig. 3. The nasal capsule in *Onychorhynchus, Platyrinchus,* and *Cnipodectes* (anterior end of skull to left; skulls viewed laterally, 1, 3, 5, 7, and ventrally 2, 4, 6, 8; magnification = 7×): **(1, 2)** *Onychorhynchus coronatus,* AMNH 14163; **(3, 4)** *Platyrinchus leucoryphus,* UMMZ 200851; **(5, 6)** *P. saturatus,* LSU 100949; **(7, 8)** *Cnipodectes subbrunneus,* AMNH 14159. Arrows indicate knifelike ventral edge of nasal septum.

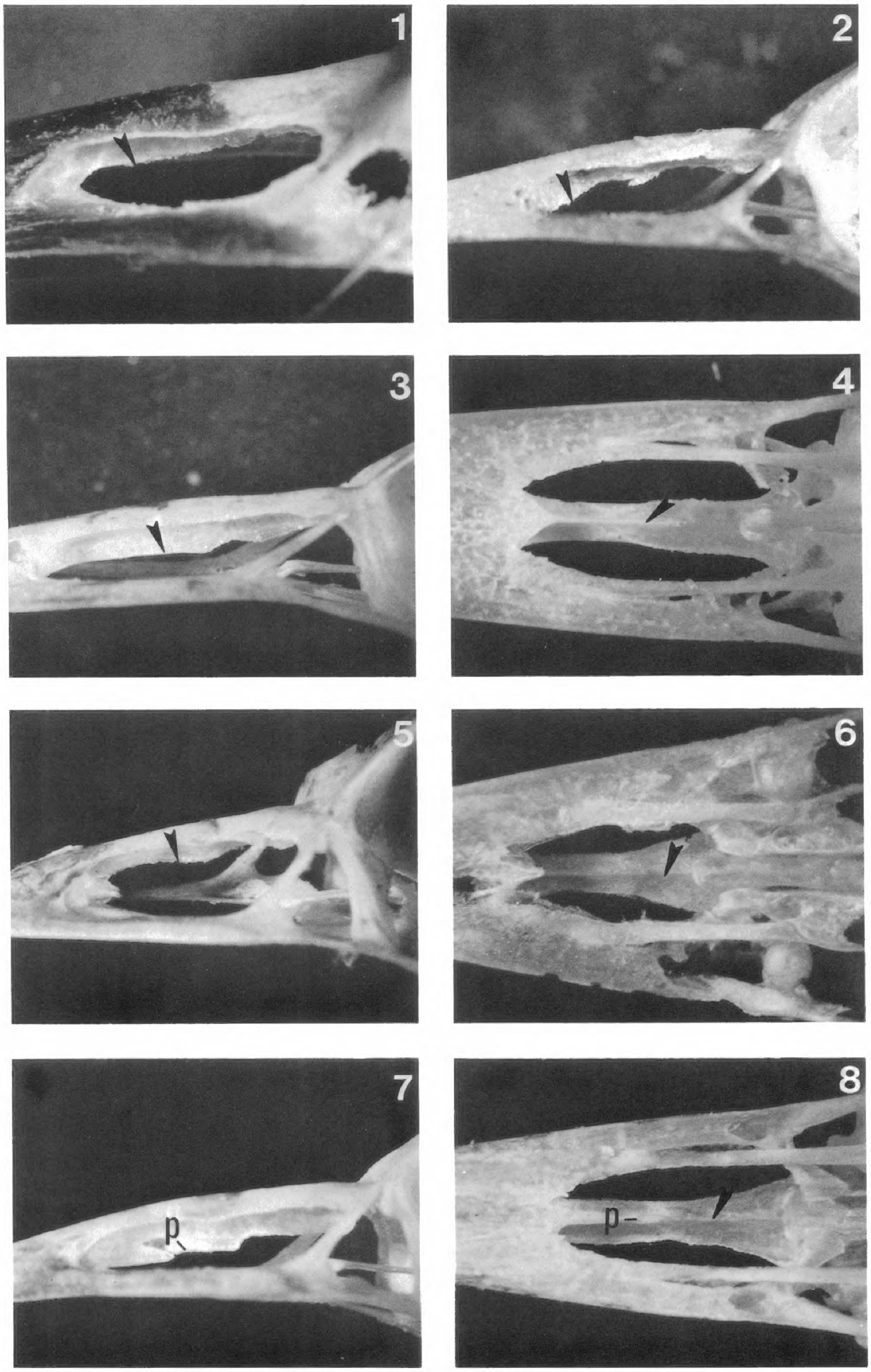

Fig. 4. The nasal capsule in *Todirostrum* and *Poecilotriccus* (anterior end of skull to left; skulls viewed laterally, 1, 2, 3, 5, 7, and ventrally, 4, 6, 8; magnification = 6×): (**1**) *T. sylvia,* LSU 50820; (**2**) *T. chrysocrotaphum,* UMMZ 200608; (**3, 4**) *T. cinereum,* AMNH 7182; (**5, 6**) *Poecilotriccus albifacies,* FMNH 323180; (**7, 8**) *P. ruficeps,* LSU 90056. Arrows indicate knifelike ventral edge of nasal septum; **p** = suggestion of a trabecular plate within the septum.

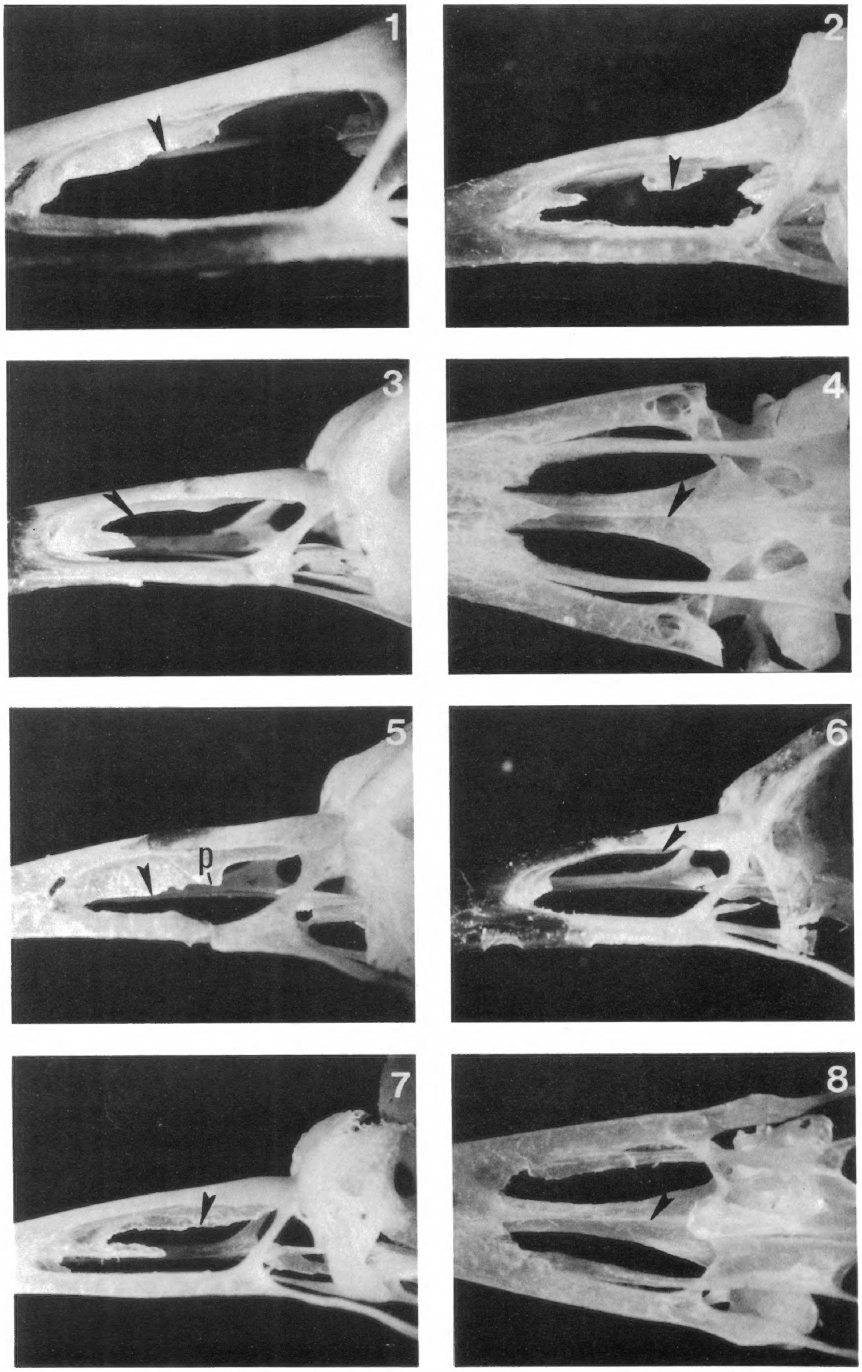

Fig. 5. The nasal capsule in *Hemitriccus* and *Myiornis* (anterior end of skull to left; skulls viewed laterally, 1, 2, 3, 5, 6, 7, and ventrally 4, 8; magnification = 6 ×, except 8 × in 1): **(1)** *H. flammulatus*, AMNH 14162; **(2)** *H. granadensis*, AMNH 14161; **(3, 4)** *H. zosterops*, LSU 118272; **(5)** *H. diops*, UMMZ 200865; **(6)** *M. ecaudatus*, LSU 73120; **(7, 8)** *M. auricularis*, UMMZ 158811. Labels as in figure 4.

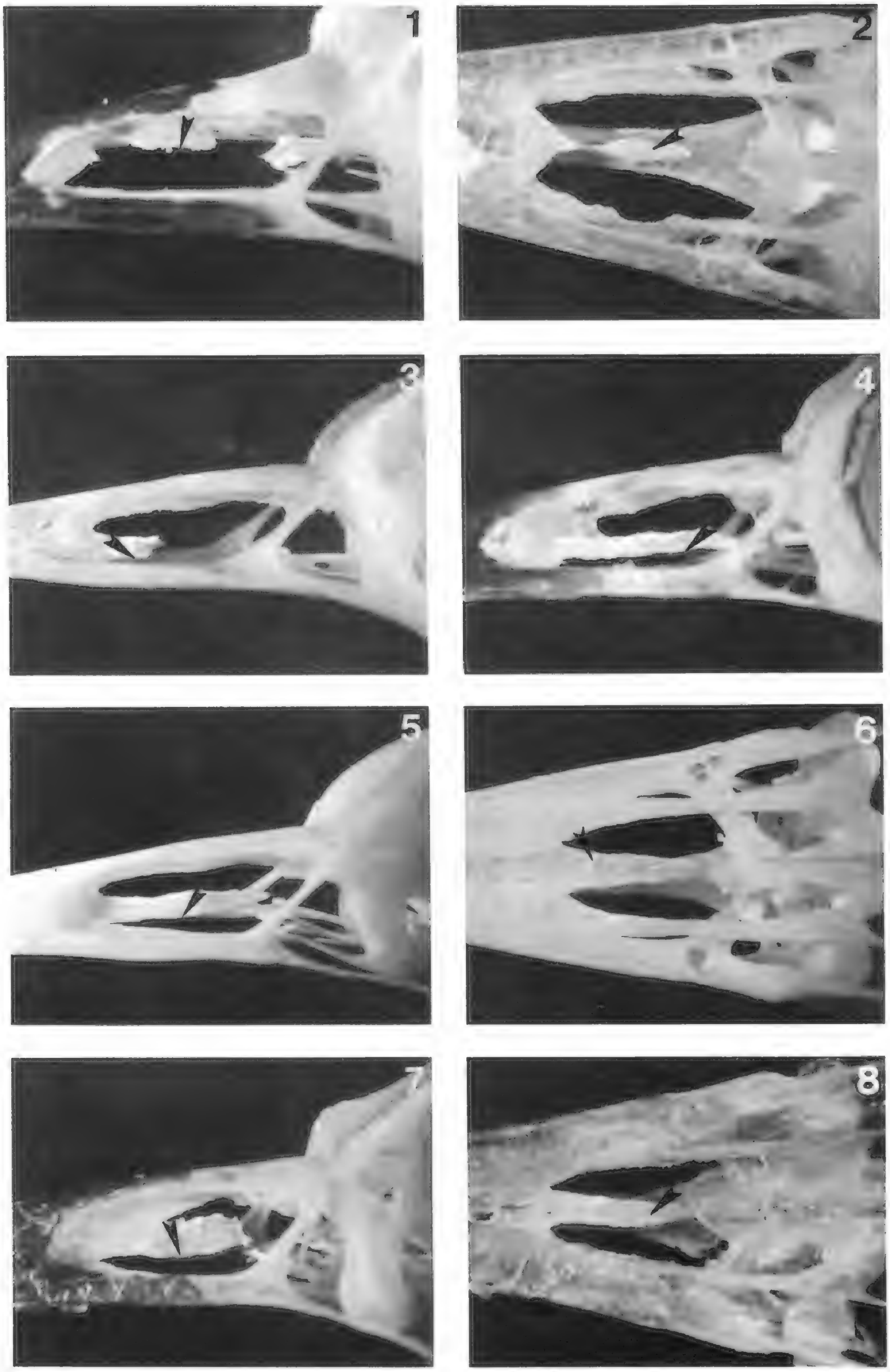

Fig. 6. Intrageneric variation in the nasal capsule in *Hemitriccus* (anterior end of skull to left; skulls viewed laterally, 1, 3, 4, 5, 7, and ventrally, 2, 6, 8; magnification = 6×): **(1, 2)** *H. rufigularis,* FMNH 315972; **(3)** *H. margaritaceiventer,* UMMZ 200862; **(4)** *H. iohannis,* FMNH 315968; **(5, 6)** *H. margaritaceiventer,* USNM 346038; **(7, 8)** *H. striaticollis,* LSU 86572. Arrows indicate trabecular plate, within the septum in 1 and 2, basal to the septum in 3 through 8.

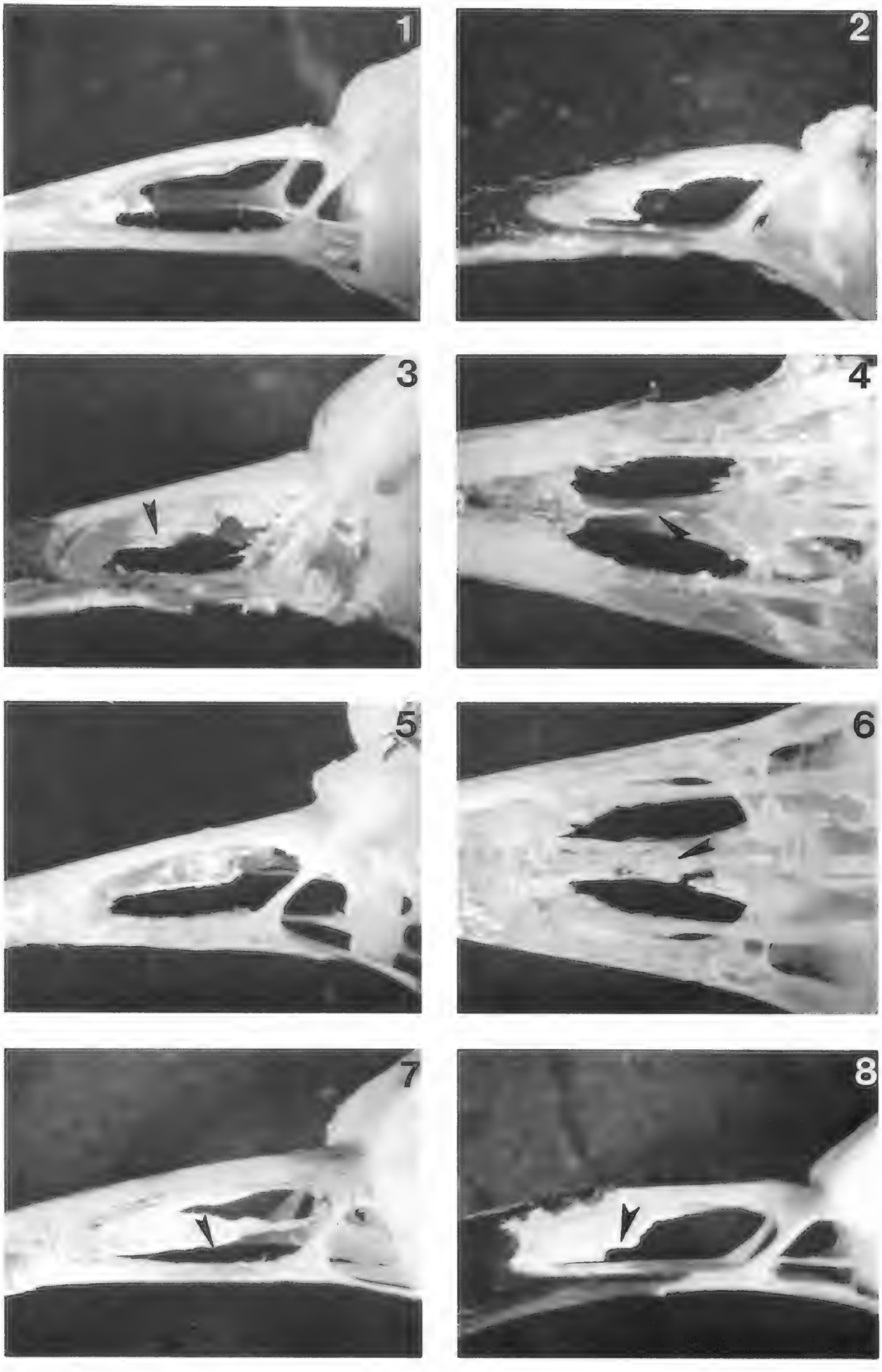

Fig. 7. The nasal capsule in *Lophotriccus, Atalotriccus,* and *Oncostoma* (anterior end of skull to left; skulls viewed laterally, 1, 2, 3, 5, 7, 8, and ventrally, 4, 6; magnification = 7 ×): **(1)** *L. pileatus,* USNM 428688; **(2)** *L. vitiosus,* LSU 64861; **(3, 4)** *L. vitiosus,* LSU 111580; **(5)** *L. galeatus,* USNM 344212; **(6, 7)** *A. pilaris,* AMNH 9034; **(8)** *O. cinereigulare,* AMNH 12750. Arrows indicate suggestion of a trabecular plate within the septum in 3, 4, and 8, and a well-developed plate basal to the septum in 6 and 7.

He specifically mentioned *Todirostrum, Euscarthmus* (now *Hemitriccus*), *Orchilus* (now *Myiornis*), *Rhynchocyclus,* and *Platyrinchus.* His identification of the *Platyrinchus* nest has been questioned by subsequent authors, however, and *Platyrinchus* is now known to build a cup nest, discussed in greater detail below.

Pendant, enclosed nests similar to that described above for the flatbills and tody-tyrants have been reported thus far for only four other genera of tyrant flycatchers. Our only knowledge of *Silvicultrix*' nesting habits comes from an early description by Taczanowski (1879) for one of the three species: "The nest has the shape of an elongated pear; the entrance is on the underside, slightly to one side" (from a translation by Morris D. Williams, personal commun.). However, the more conservative characters of the nasal septum conflict with this behavioral character. *Silvicultrix* shares the uniquely derived characteristics of the nasal septum in my *Empidonax* assemblage (Lanyon, 1986). If this description of the nest form is substantiated by additional accounts, than the parsimonious interpretation is that this nest form has evolved convergently in *Silvicultrix. Myiobius* (including *Terenotriccus*) is also a member of my *Empidonax* assemblage (Lanyon, 1988b) and is reported to have a pendant, globular nest with side entrance (Euler, 1900; Ihering, 1904; Carriker, 1910; Huber, 1932; Skutch, 1960; Gross, 1950; Wetmore, 1972). Though the nasal septum and associated trabecular plate of *Myiobius* exhibit some notable deviations from the normal-appearing nasal capsule in *Empidonax* and allies, it is easier to relate these structures to those of that assemblage than to the poorly ossified capsule of the flatbills and tody-tyrants, implying an independent evolution of this nest form in *Myiobius.* The other two genera with a similar nest form are *Mionectes* and *Leptopogon,* but these likewise have a more derived nasal capsule and I have hypothesized that they developed this nesting behavior convergently within my *Elaenia* assemblage (Lanyon, 1988a).

Clearly, the overall similarity that one sees in the nasal capsules within this assemblage could be attributed to their simplicity and the lack of obvious specializations that are apparent at once when one examines the skulls of the other tyrant assemblages. Though the similarity in these nasal capsules may in fact be due to a derived state, there is at least the spectre of primitiveness, and one is hesitant to place confidence in this character state (character 1) as the sole evidence for monophyly. However, the confidence limits are increased greatly when the use of this character is combined with the more certainly derived states of the interorbital septum (character 2) and nest form (character 3). I interpret characters 1–3, taken collectively, to be a strong argument that the flatbills and tody-tyrants have had a common ancestry (fig. 1).

THE PUTATIVE RELATIVES

Ramphotrigon

Zimmer's (1939) transfer of *megacephalus* out of *Tolmomyias* and into *Ramphotrigon* is supported by syringeal and cranial morphology, as well as by nesting behavior, as I have discussed previously (Lanyon, 1985). The genus *Ramphotrigon,* now consisting of *megacephala, ruficauda,* and *fuscicauda,* historically has been merged with *Rhynchocyclus* (Sclater, 1888) or has been recognized but considered a close relative of *Rhynchocyclus* and the other flatbills (Berlepsch, 1907; Hellmayr, 1927; Zimmer, MS; Traylor, 1977; Traylor and Fitzpatrick, 1982). I have presented arguments based on cranial and syringeal morphology and nesting behavior that *Ramphotrigon* is not a flatbill, but is part of the myiarchine lineage, with *Deltarhynchus* its closest relative (Lanyon, 1985). The diagnostic myiarchine nasal capsule of *Ramphotrigon,* nearly fully ossified and with a conspicuous internal supporting rod, can be seen in figure 11: 1, 2.

Pseudotriccus

The only species traditionally placed among the tody-tyrants (Sclater, 1888; Berlepsch, 1907; Hellmayr, 1927; Zimmer, 1940, MS; Meyer de Schauensee, 1966) but omitted from my assemblage here are the three that Traylor (1979) currently assigns to the genus *Pseudotriccus.* Traylor (1977) remarked that this genus "seems to have no close relatives . . . . It has generally been associated with *Hemitriccus* at the end of the *Todirostrum* group,

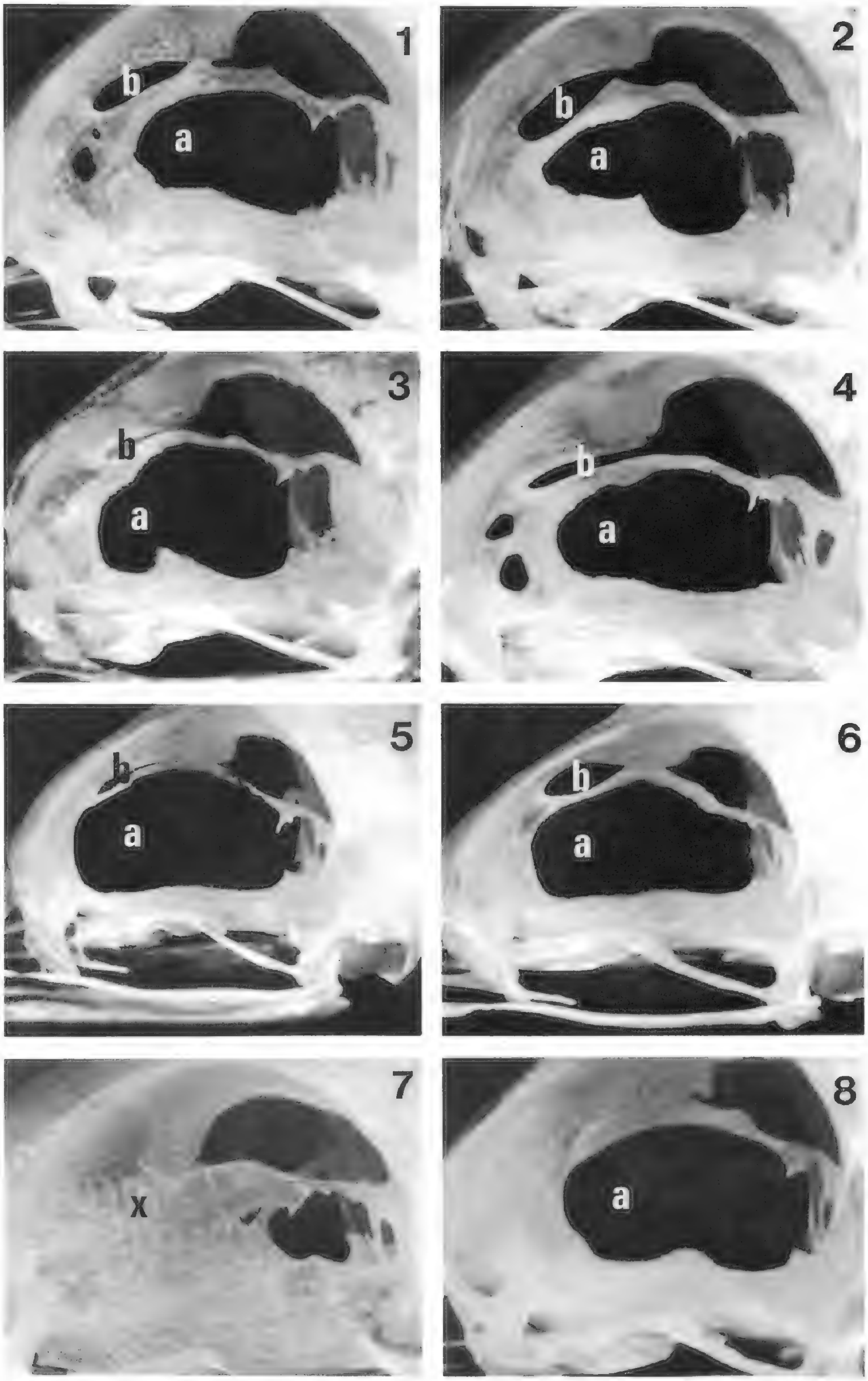

Fig. 8. Intergeneric variation in the interorbital septum among the flatbills (anterior end of skull to left; lateral views; magnification = 4×, except 5× in 3, 4, and 7): (**1**) *Rhynchocyclus brevirostris,* AMNH 14478; (**2**) *R. olivaceus,* FMNH 315975; (**3**) *Tolmomyias poliocephalus,* FMNH 315990; (**4**) *T. sulphurescens,* AMNH 10307; (**5**) *Platyrinchus coronatus,* AMNH 15213; (**6**) *P. saturatus,* LSU 100949; (**7**) *Onychorhynchus coronatus,* AMNH 14163; (**8**) *Cnipodectes subbrunneus,* AMNH 14159. **a** = infraorbital fenestra; **b** = remnant of supraorbital fenestra; **x** = septum fully ossified, no fenestrae, in *Onychorhynchus.*

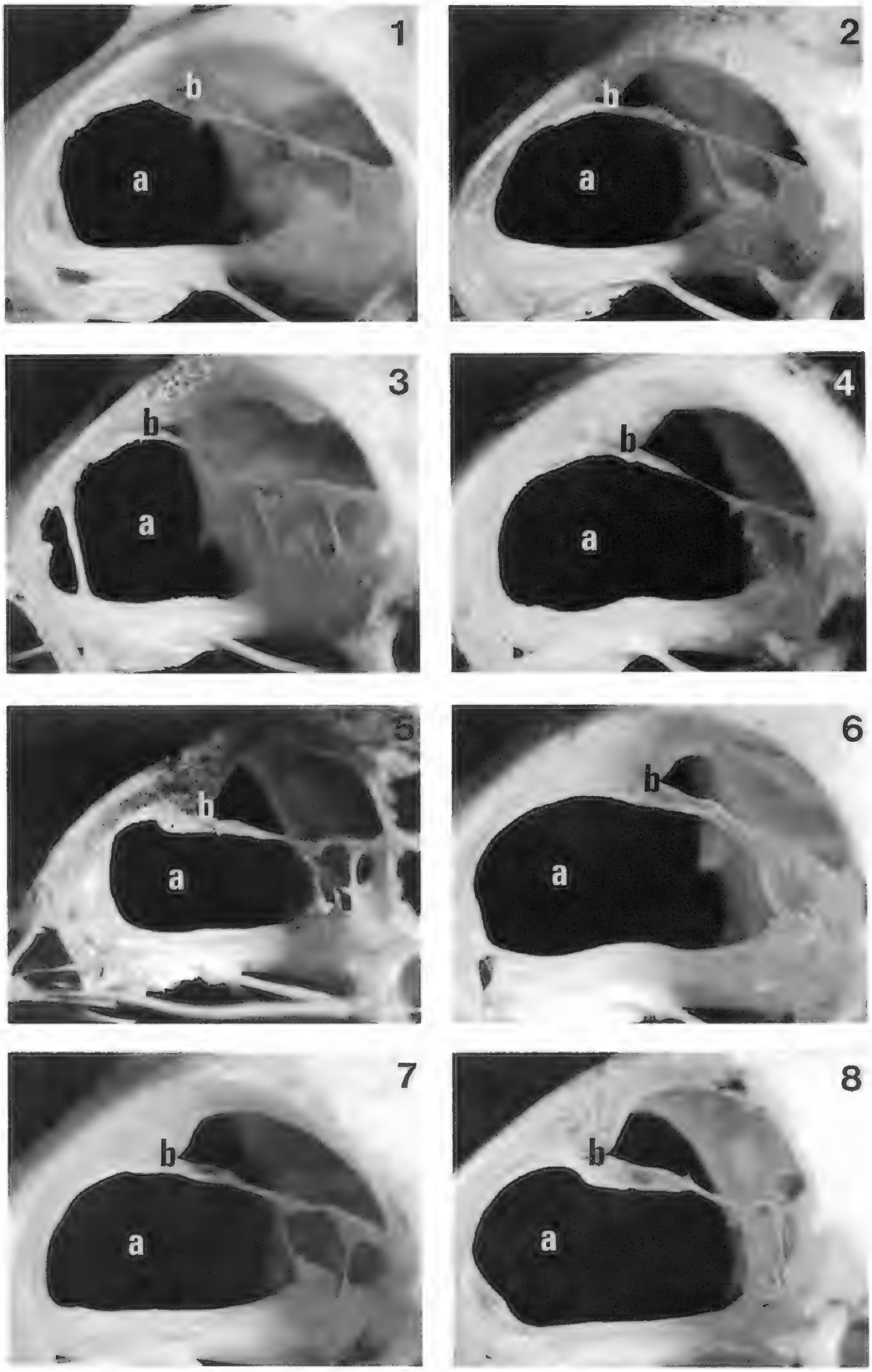

Fig. 9. Intergeneric variation in the interorbital septum among the tody-tyrants (anterior end of skull to left; lateral views; magnification = 6×): (**1**) *Todirostrum sylvia,* LSU 50820; (**2**) *T. cinereum,* AMNH 7182; (**3**) *Poecilotriccus ruficeps,* LSU 90057; (**4**) *Lophotriccus vitiosus,* LSU 111580; (**5**) *Myiornis ecaudatus,* LSU 73120; (**6**) *Hemitriccus flammulatus,* AMNH 14162; (**7**) *Hemitriccus zosterops,* LSU 118272; (**8**) *Oncostoma cinereigulare,* AMNH 11707. **a** = infraorbital fenestra; **b** = remnant of supraorbital fenestra.

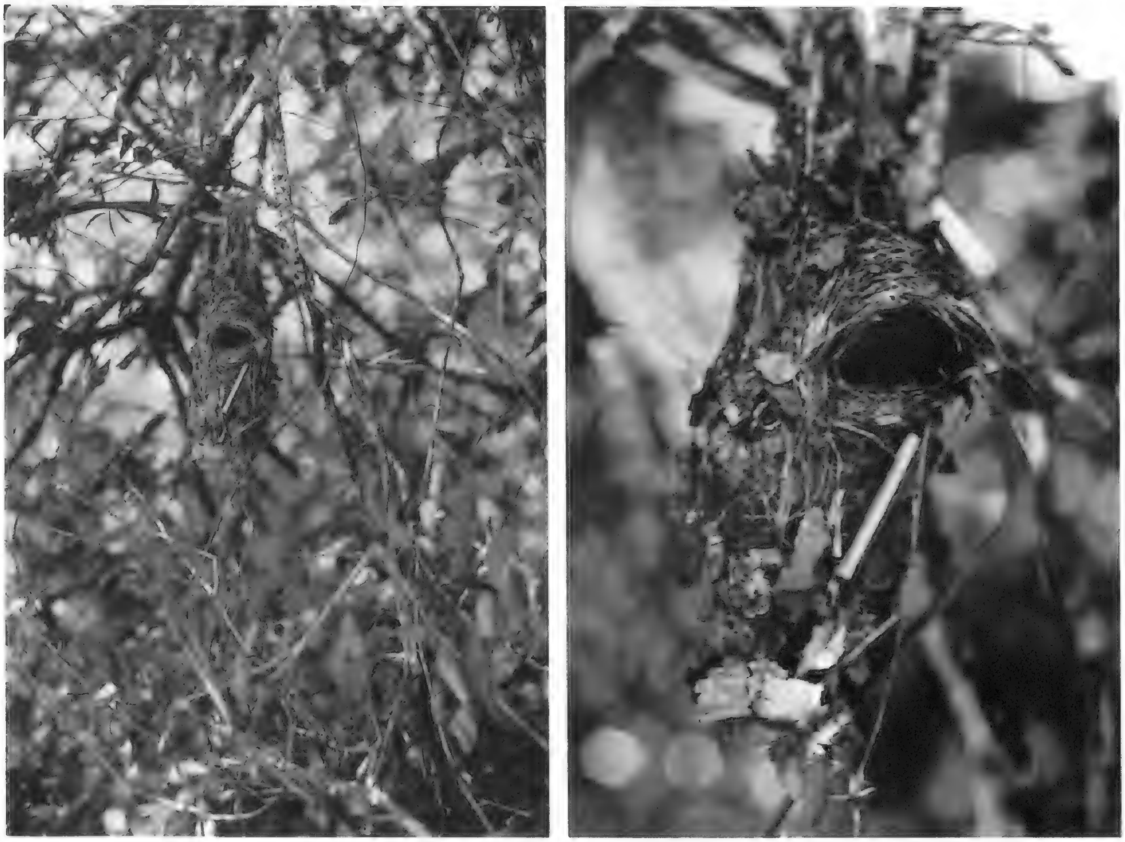

Fig. 10. Enclosed, pendant nest of *Hemitriccus margaritaceiventer,* photographed by the author at Las Tres Marías, Corrientes, Argentina, on Nov. 18, 1970, is typical of the nests that have been reported for the flatbills and tody-tyrants. The spherical side opening, with small visorlike projection above, was 2 m from the ground. An adult female (AMNH 816976) and an eight-day-old nestling (AMNH 816977) were collected at the nest.

but there is little real resemblance." Traylor (1977, 1979) and Traylor and Fitzpatrick (1982) removed *Pseudotriccus* from their tody-tyrant group and placed it in a "transitional group" nearby.

The syrinx of *Pseudotriccus* does not share either of the uniquely derived character states that characterize the tody-tyrants, as discussed below. A broad, calcified pessulus of distinctive shape is one of the more conspicuous features of the *Pseudotriccus* syrinx (fig. 11: 7, 8) and is perceived here to be a derived character shared with *Corythopis.* The nasal capsule in *Pseudotriccus* skulls typically is more fully ossified than that of the tody-tyrants and bears a small trabecular plate, located well within the septum (fig. 11: 3, 4). The nest of *Pseudotriccus* has not been reported, but that of its presumed closest relative, *Corythopis,* is an oven-shaped structure (with side entrance) located on the ground (Oniki and Willis, 1980). I have argued in detail elsewhere that *Pseudotriccus* is a member of my *Elaenia* assemblage (Lanyon, 1988a).

RELATIONSHIPS WITHIN THE ASSEMBLAGE

If one accepts the argument for monophyly, then the 10 genera that I recognize within the assemblage can be grouped into an unresolved trichotomy according to the basic morphology of the syrinx, as illustrated in the phylogenetic diagram in figure 1. In *Rhyn-*

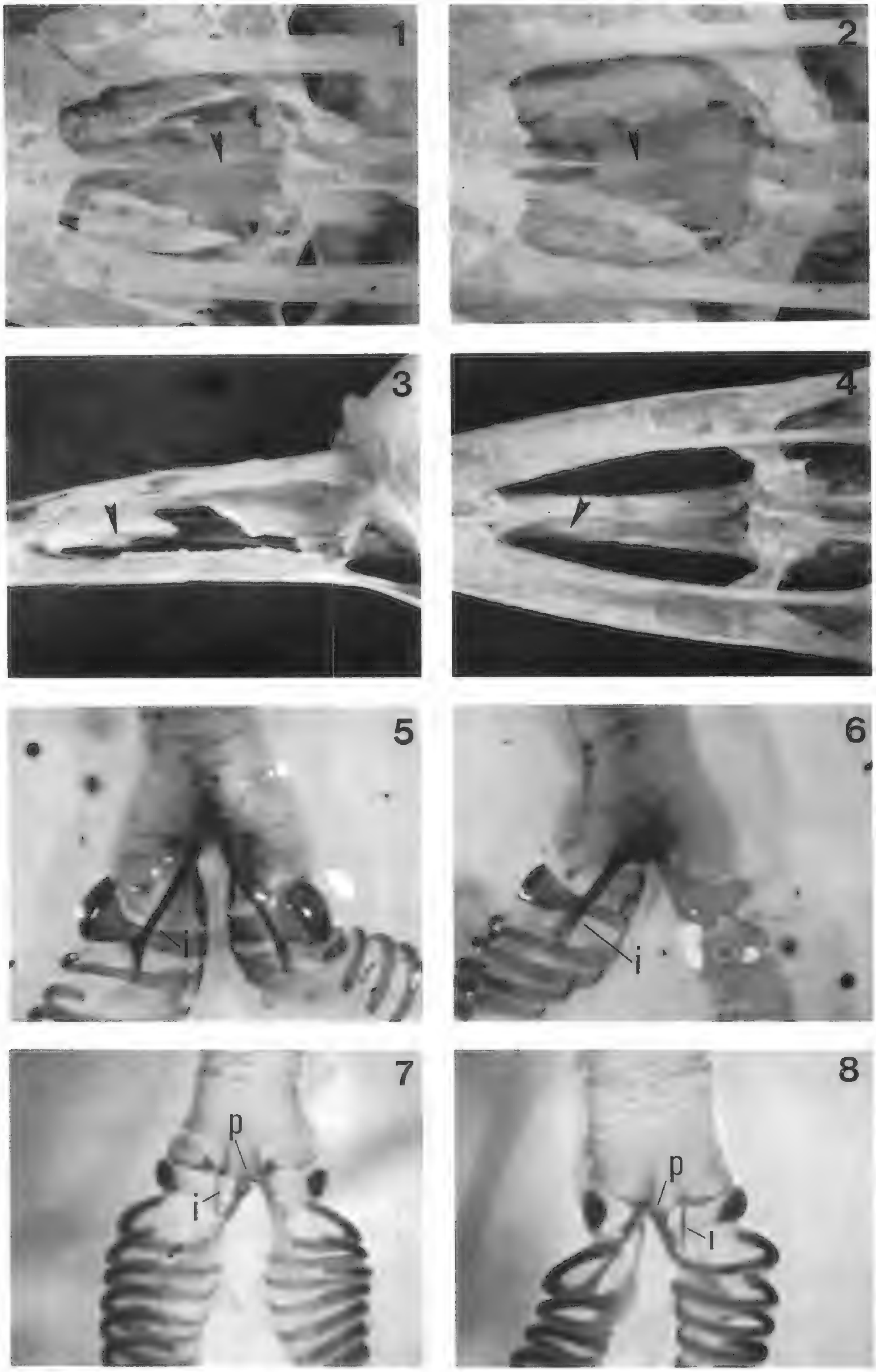

Fig. 11. The nasal capsules and syringes of putative relatives of the flatbills and tody-tyrants (anterior ends of skulls to the left; magnification = 6×, except 9× in 2; syringes viewed from dorsal aspect, magnification = 9× in 5, 6, and 12× in 7, 8): (**1**) ventral view of capsule of *Ramphotrigon fuscicauda,* LSU 101510; (**2**) ventral view of capsule of *R. megacephala,* LSU 101512; (**3, 4**) lateral and ventral views of capsule of *Pseudotriccus ruficeps,* AMNH 6937; (**5**) syrinx of *Ramphotrigon megacephala,* LSU 102610; (**6**) syrinx of *R. fuscicauda,* LSU 102608; (**7**) syrinx of *Pseudotriccus pelzelni,* UK 69000; (**8**) syrinx of *Pseudotriccus simplex,* LSU 98046. Arrows point to conspicuous internal supporting rod in fully ossified capsule of *Ramphotrigon,* and to small trabecular plate located within the nasal septum of *Pseudotriccus*; **p** = broad, calcified pessulus; **i** = internal cartilages.

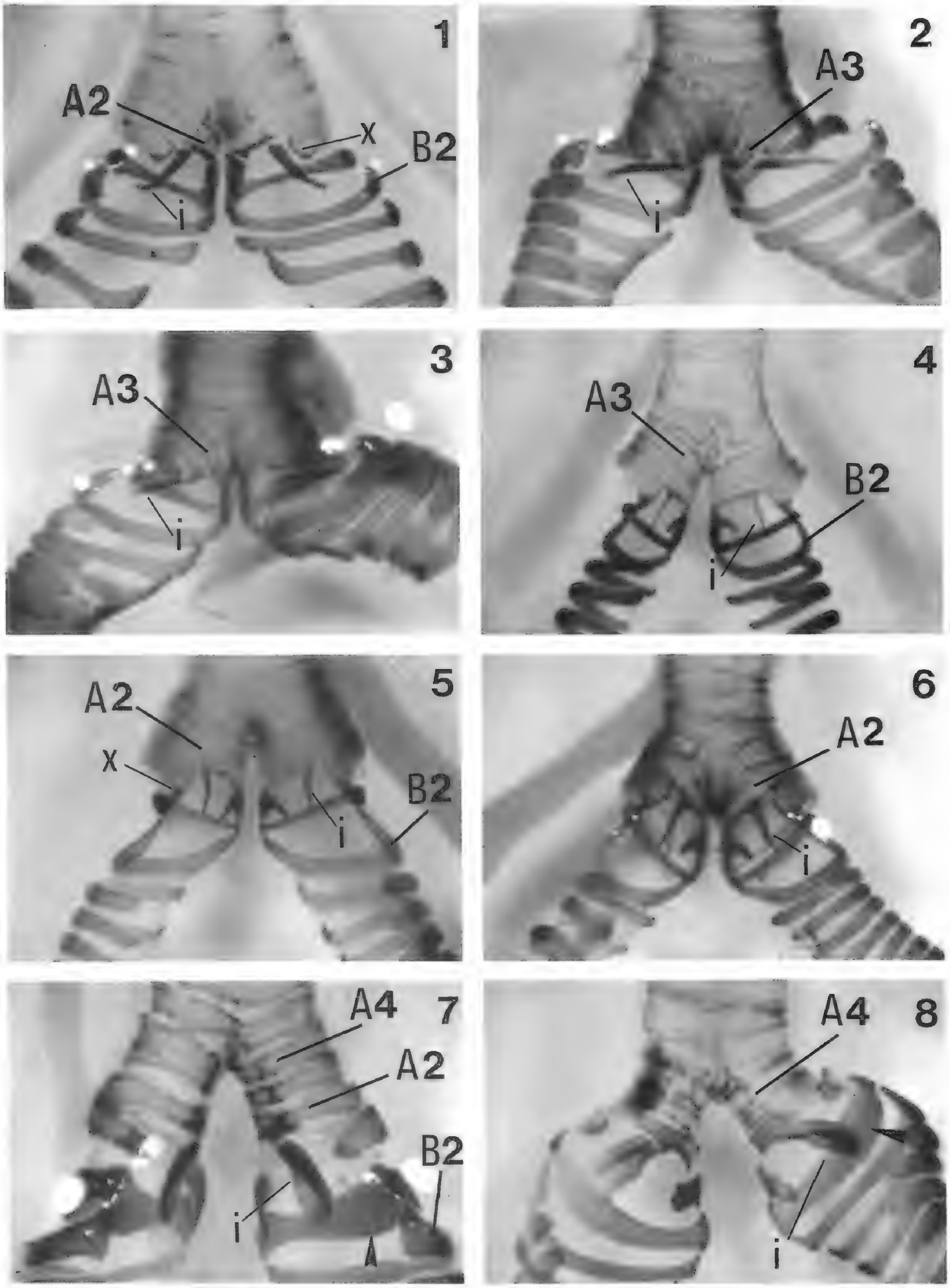

Fig. 12. The syringes of *Rhynchocyclus*, *Tolmomyias*, and *Onychorhynchus* (dorsal aspect; magnification = 14×): (1) *Rhynchocyclus fulvipectus*, LSU 89487; (2) *R. olivaceus*, LSU 108485; (3) *R. brevirostris*, LSU 108488; (4) *Tolmomyias sulphurescens*, AMNH 6814; (5) *T. assimilis*, LSU 71473; (6) *T. poliocephalus*, FMNH 290389; (7) *Onychorhynchus coronatus*, AMNH 8781; (8) *O. coronatus*, LSU 102588. A and B elements as labeled; **i** = internal cartilages; **x** = cartilaginous ventromedial end of A1; arrows point to broad central regions of B1s.

chocyclus, Tolmomyias, Onychorhynchus, and *Platyrinchus* there is at least one A element that forms a complete, calcified ring around each bronchus (character 4). The monotypic *Cnipodectes* stands alone in having no complete A ring around either bronchus and in lacking the uniquely derived syringeal characters that are shared by the tody-tyrants. The five genera of tody-tyrants cluster by virtue of syringeal characters that are unique among all tyrant flycatchers and discussed more fully below.

Rhynchocyclus and *Tolmomyias*

The species that Hellmayr (1927) placed in his new genus *Tolmomyias* historically had been included in *Rhynchocyclus* (Sclater, 1888; Berlepsch, 1907); since Hellmayr, all workers have recognized the two genera but continued to consider them closely allied (Zimmer, MS; Traylor, 1977). However, Ames (1971) reported strong differences in their syringeal morphology that he believed raised serious questions about the reliability of external morphology for revealing relatedness. The close relationship of *Rhynchocyclus* and *Tolmomyias* with the other flatbills, including *Ramphotrigon*, has not been challenged seriously since Hellmayr (1927) placed them all in one subfamily.

I have a series of seven *Rhynchocyclus* skulls (representing all three species) and 12 *Tolmomyias* skulls (representing all four species). The nasal septum is nearly completely unossified in both of these genera (character 1). Though the appearance of the nasal region is basically the same in the two series, there is, on average, slightly more nasal septum projecting ventrally from the roof of the capsule in the *Rhynchocyclus* skulls (fig. 2: 1–4), and slightly more alinasal wall ossified (dorsomedially) in the *Tolmomyias* skulls (fig. 2: 5–8). There is no suggestion of a transverse trabecular plate in either series. In both genera the interorbital septum is largely unossified (character 2); the infraorbital fenestra is somewhat smaller than in the tody-tyrants, *Platyrinchus* and *Cnipodectes,* while the supraorbital fenestra is slightly larger, on average, than in those genera (fig. 8).

In my sample of *Rhynchocyclus* syringes (7 specimens of the 3 species) and of *Tolmomyias* syringes (11 specimens of the 4 species), the basic configuration of the tracheobronchial junction is identical and some specimens would not be identifiable to genus on this character alone (fig. 12: 1–6). At least one A element (usually the A2) is complete around each bronchus and calcified (character 4). In some specimens the A3s as well as the A2s may be complete and calcified, or these elements may fuse into a single complete band medially in each bronchus. In some *Rhynchocyclus* only the A3s may be complete, and these may be either calcified or partly cartilaginous medially; in other *Rhynchocyclus* both the A3s and the A4s are complete and calcified. All of my specimens have a narrow calcified pessulus derived from the A4s, or sometimes from the A5s. The internal cartilages in both genera are narrow and basically linear in shape (character 5).

That *Rhynchocyclus* and *Tolmomyias* may be each other's closest relative is suggested by an embellishment of the enclosed nest, which, as far as is presently known, is unique within the family. Their nests are retort-shaped, with the entrance at the end of a downward pointing tube or spout projecting from the side (character 6) (AMNH collection; Ihering, 1904; Carriker, 1910; Chubb, 1910; Cherrie, 1916; Todd and Carriker, 1922; Dickey and Van Rossem, 1938; Haverschmidt, 1950, 1968, 1974; Skutch, 1960; Herklots, 1961; Rowley, 1966, 1984; ffrench, 1976; Thurber, 1978). Though Skutch (1960) has made a point of the eggs of these two genera being different, the published descriptions suggest considerable overlap, and range from pinkish white to a bright salmon-orange or reddish-brown, mottled with darker reddish-brown around the thicker end (AMNH collection; Oates and Reid, 1903; Carriker, 1910; Cherrie, 1916; Todd and Carriker, 1922; Haverschmidt, 1950, 1968, 1974; Herklots, 1961; Rowley, 1966). However, the two genera are separable by consistent differences in two syringeal characters: (1) the position of the internal cartilages and (2) the shape of the cartilage at the ventral ends of the A1 elements. In *Rhynchocyclus* the rather narrow internal cartilages are free within the internal tympaniform membrane (i.e., not attached to any elements) and located in close proximity to the dorsal ends of the A1s, but extending well beyond those elements (character 7), and the cartilaginous ventromedial ends of the A1s are broad and blunt (character 8) (best seen in fig. 12: 1). In *Tolmomyias* the rather narrow internal cartilages are attached to the dorsomedial segments of the A2 elements, are located further from the dorsal ends of the A1s, and do not extend appreciably beyond those elements (character 9), and the cartilaginous ventromedial ends of the A1s are more delicate and curvilinear in shape (character 10) (best seen in fig. 12: 5). Thus I can confirm Ames' (1971) findings of syringeal differences between these genera, but these differences are no greater than those I have found between sister taxa in other lineages of tyrant flycatchers. They do not argue against a close relationship of *Rhynchocyclus* and *Tolmomyias,* but support Skutch's (1960) position, based on differences in mating behavior, egg color, and natal down, that their separate generic status be retained.

Onychorhynchus and *Platyrinchus*

Historically there has been considerable doubt and disagreement as to the phylogenetic position of *Onychorhynchus* and *Platyrinchus.* At no time has it been implied that they might be each other's closest relative.

Both Sclater (1888) and Berlepsch (1907) assigned *Onychorhynchus* to a subfamily separate from that of either the flatbills (in which these authors placed *Platyrinchus*) or the tody-tyrants. Even Hellmayr (1927) maintained *Onychorhynchus* next to *Hirundinea* in the Myiarchinae. Warter (1965) appears to have been the first to suggest that *Onychorhynchus* might have affinities with the flatbills; he recommended that it be given tribal status within a subfamily that also included separate tribes for the flatbills and the tody-tyrants. Ames (1971) could see no relationship between *Onychorhynchus* and either the tody-tyrants or the flatbills, on the basis of syringeal morphology, and chose to place it in a group with *Myiobius* and its allies. Traylor (1977) acknowledged Warter's findings but placed more credence on the syringeal evidence and chose to keep *Onychorhynchus* near *Myiobius,* in a subfamily separate from that containing the flatbills and tody-tyrants. As recently as 1982, Traylor and Fitzpatrick regarded *Onychorhynchus* as a member of their "*Myiobius* group," in a subfamily different from that of the flatbills and tody-tyrants.

Sclater (1888) and Berlepsch (1907) placed *Platyrinchus* next to the tody-tyrants, while Hellmayr (1927) allied it with the flatbills. Traylor (1977) was impressed with the fact that *Platyrinchus* builds cup-shaped rather than pendant nests and remarked that it "does not seem closely related to any of the other genera [of flatbills]"; he placed it at the end of his Elaeniinae, following the flatbills.

The nasal region of the skull in my seven specimens of the monotypic *Onychorhynchus* is like that of the other flatbills. There is only a remnant of the nasal septum, located medially along the roof of the capsule and heavily buttressed laterally (character 1) (fig. 3: 1, 2). The interorbital septum is fully ossified, however, with nothing remaining of either interorbital fenestra (character 13) (fig. 8: 7), quite unlike the poorly ossified interorbital septum in the rest of the flatbills and tody-tyrants (figs. 8, 9). *Onychorhynchus* is the only genus within the assemblage that lacks character 2. The 18 specimens that I have examined of 6 of the 7 species of *Platyrinchus* have nasal septa (fig. 3: 3–6) like those of my series of *Onychorhynchus*. Using only the nasal septum as a criterion, the skulls of the two genera could not be identified to genus with certainty. *Platyrinchus* skulls have the typical flatbill and tody-tyrant "type 4" interorbital septum (character 2), however, in which the infraorbital fenestra is much enlarged and the supraorbital fenestra is nearly obliterated (fig. 8: 5, 6).

The nest of *Onychorhynchus* is of the pendant, enclosed variety, and differs from nests of its allies only by being exceptionally long, i.e., from 2 to 6 ft (character 14) (Carriker, 1910; Todd and Carriker, 1922; Skutch, 1960; Haverschmidt, 1968; Wetmore, 1972). The eggs are unusually dark reddish or chocolate brown (Carriker, 1910; Skutch, 1960; Haverschmidt, 1968; Wetmore, 1972). *Cnipodectes* is the only other tyrant reported to have a pendant nest of comparable length. Ihering (1900) initially described the nest of *Platyrinchus mystaceus* as a bowl, but later (1902) corrected his "mistake" and described a pendant, purse-shaped nest for this species. All reliable reports subsequently for *mystaceus* and *coronatus* (the only two *Platyrinchus* for which the nest is known) are of a compact, open, cup-shaped nest in a fork or crotch (Carriker, 1910; Todd and Carriker, 1922; Skutch, 1960; ffrench, 1976; Rowley, 1984). *Platyrinchus* is the only genus within the assemblage that lacks character 3.

I have a series of four syringes of *Onychorhynchus*, representing populations from Mexico to Peru (fig. 12: 7, 8). The basic configuration of the tracheobronchial junction is the same as that in *Rhynchocyclus, Tolmomyias,* and *Platyrinchus* (character 4). There are two or more A elements forming complete supporting rings around each bronchus. In one specimen only the A2s and A3s provide this support, with the A4s contributing to the calcified pessulus. In another specimen, in addition to the two complete A2s, the A3 and A4 elements are fused into a single complete ring around one bronchus, while these elements form two independent rings around the other bronchus. In two of the four specimens, there are three independent and complete rings (A2s, A3s, and A4s) around each bronchus (best seen in fig. 12: 7), and the calcified pessulus is continuous with the A5 elements. These complete A rings are usually calcified, though in two specimens a small medial segment of the A2s is still cartilaginous. The internal cartilages are very broad and shaped like a spatula or a child's mitten, with the dorsal edge somewhat thickened to accommodate the "thumb" (character 11) (fig. 12: 7, 8). These cartilages are attached to the medial segments of the A2s. Additionally, the B1 elements are very broad in their central regions (character 12), but of nearly uniform width in *Rhynchocyclus* and *Tolmomyias.* Ames (1971) reported the absence of intrinsic muscles in the syrinx of *Onychorhynchus* (character 15), whereas *Platyrinchus, Rhynchocyclus,* and *Tolmomyias* each have a single pair; I can confirm these differences, even though my specimens have been cleared.

My series of syringes from *Platyrinchus* (12 specimens examined, representing 5 of the 7 species; *flavigularis* and *leucoryphus* lacking) also has the basic configuration of the tracheobronchial junction of the other flatbills (character 4), but only the A3 element is complete around each bronchus. The calcified pessulus is narrow and continuous with the A4s. Surprisingly, there was considerable intrageneric variation in these syringes—more than I have come to expect within tyrant genera. Four (*mystaceus, saturatus, cancrominus,* and *platyrhynchos*) of the five species examined have internal cartilages that are very broad and spatula-shaped, as in *Onychorhynchus* (character 11), and the B1 elements are very broad in their central regions (character 12) (fig. 13: 1–4). All four of these species have the broad internal cartilages partly ossified and connected to the dorsal ends of the A1s and A2s and to the medial segments of the A3s (character 16), and the B2s are forked ventrally (character 17) (fig. 13: 1–4). In my one well-preserved specimen of *platyrhynchos,* the internal cartilages are less extensively ossified and somewhat more amorphous in shape than in the other three species, the pessulus is considerably broader in width, and the A2s have cartilaginous medial segments confluent with the calcified medial portion of the A3s (fig. 13: 4). My three specimens of *coronatus* (from Nicaragua, Bolivia, and eastern Brazil) have the same configuration of the tracheobronchial junction (character 4) as the other species of *Platyrinchus,* with only the A3 elements complete around each bronchus, but they differ markedly in having internal cartilages that are narrower, not spatula-shaped, and that are conspicuously forked distally. Additionally these three specimens of *coronatus* lack characters 12 and 17, i.e., the B1 elements are not broad in their central regions and the B2s are not forked distally (fig. 13: 5, 6). This significant departure in syringeal morphology of *coronatus* from that of the other species of *Platyrinchus* certainly merits further investigation, but is beyond the scope and objectives of this study. One might inquire as to whether *coronatus* has also diverged similarly with respect to its behavior and ecology.

If one accepts the admittance of both *Onychorhynchus* and *Platyrinchus* to the assemblage, similarities in the basic configuration of the tracheobronchial junction and in the shape and position of the internal cartilages take on greater significance. That they may well be sister taxa is suggested by the great similarity in their internal cartilages. They are the only genera within the assemblage to share derived characters 11 and 12.

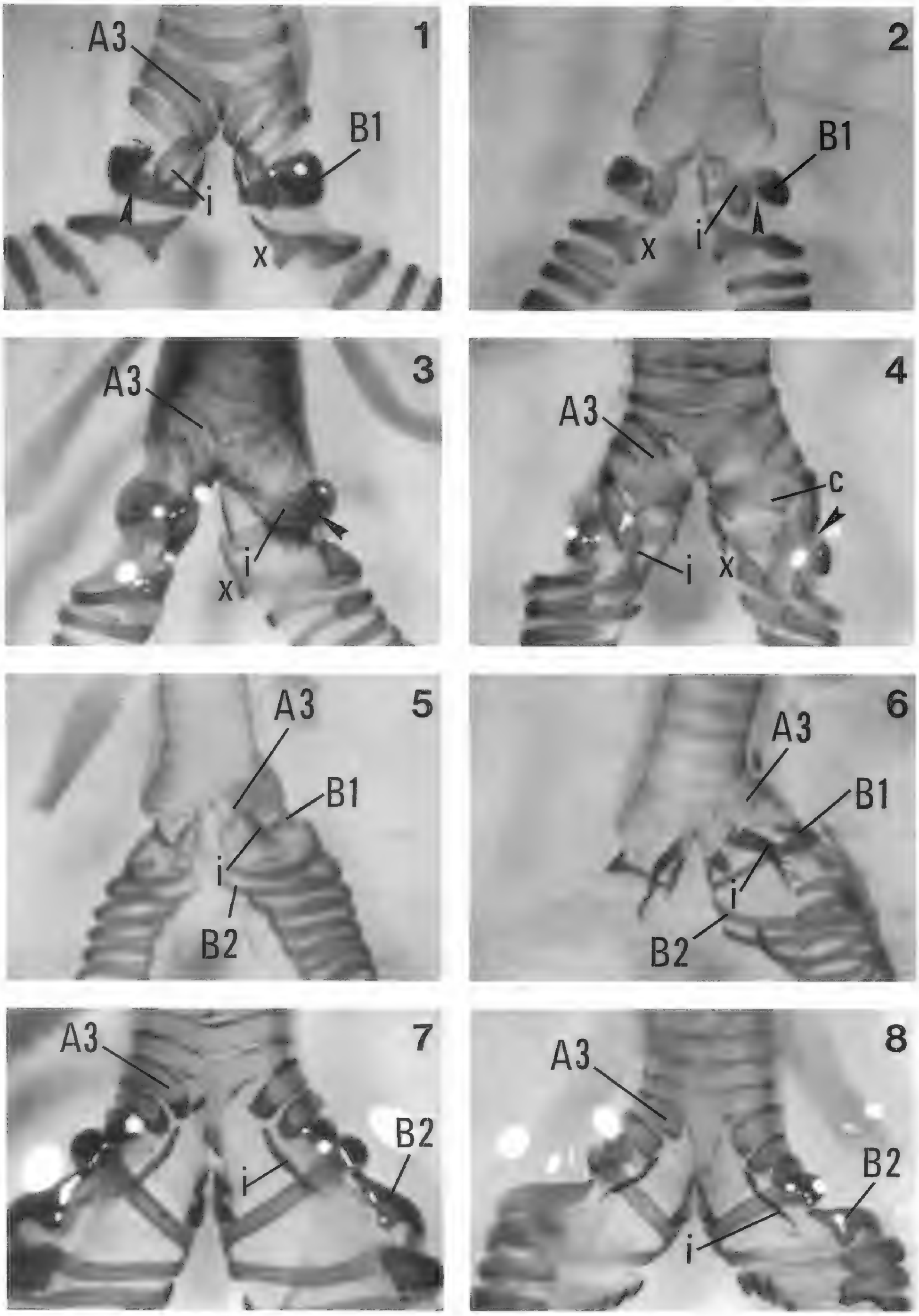

Fig. 13. The syringes of *Platyrinchus* and *Cnipodectes* (dorsal aspect; magnification = 13×): **(1)** *Platyrinchus saturatus*, AMNH 9398; **(2)** *P. mystaceus*, PMNH 2758; **(3)** *P. cancrominus*, AMNH 6729; **(4)** *P. platyrhynchos*, LSU 102593; **(5)** *P. coronatus*, MPEG 2238; **(6)** *P. coronatus*, LSU 102599; **(7)** *Cnipodectes subbruneus*, PMNH 6678; **(8)** *C. subbrunneus*, LSU 108464. A and B elements as labeled; **i** = internal cartilages; arrows point to broad central regions of B1s; **x** = ventral end of B2s; **c** = cartilaginous medial segments of the A2s.

Because there is no tradition of regarding *Onychorhynchus* as a close relative of *Rhynchocyclus* and *Tolmomyias,* one might legitimately question the wisdom of interpreting the poorly ossified nasal septum as a derived character state and inquire into alternative hypotheses of relationships. Logically one might look to other tyrant lineages in which the basic configuration of the tracheobronchial junction in the syrinx is similar to that of *Rhynchocyclus* and *Tolmomyias* (character 4). Similar configurations, i.e., in which at least one A element forms a complete ring around each bronchus, have evolved in some *Attila* and in the *Myiozetetes* branch of the kingbird lineage, but the biology of those tyrants is so completely different from that of *Onychorhynchus* that there can be no question that the similarity is due to convergence. Similar configurations of the syrinx in two other lineages cannot be dismissed so readily, however, for some of the genera involved are known to build pendant, enclosed nests like those of the flatbills; these cases require closer scrutiny.

One of these is the *Myiophobus* group in my *Empidonax* assemblage, which contains *Myiophobus, Hirundinea, Pyrrhomyias,* and *Myiobius,* all of which have the A2s and/or A3s complete around each bronchus and a calcified pessulus continuous with the A4s and/or A5s. The species of *Myiobius* build pendant, enclosed nests, have an ossified interorbital septum, heavy rictal bristles that are as long as or longer than the broad flatbills, and no intrinsic syringeal muscles. These are *Onychorhynchus* character states as well, and make a strong argument that *Myiobius* and *Onychorhynchus* are each other's closest relative, with *Onychorhynchus* having evolved a longer bill, ornamental crest, a longer nest, and some differences in the shape of the internal cartilages and the B1 elements. This treatment reflects the traditional classification of Hellmayr (1927) who, on external morphology alone, had *Onychorhynchus* grouped with *Myiobius, Myiophobus, Hirundinea,* and *Pyrrhomyias* at the end of his Myiarchinae. Traylor (1977) was impressed with Ames' placement of *Onychorhynchus* in his "*Myiobius*" group on syringeal characters, and also with the similarities in nesting behavior, and chose to place *Onychorhynchus* near *Myiobius* in a subfamily separate from that of the flatbills.

However, *Onychorhynchus* lacks the derived character states of the nasal septum that define my *Empidonax* assemblage, to which *Myiobius* is assigned (Lanyon, 1986, 1988b): the fully ossified septum, with "anterior notch" and a transverse trabecular plate along the ventral edge of the septum. In my studies of tyrant evolution there is every indication that the cranium is far more conservative than syringeal morphology, nesting biology, and external morphology. In interpreting *Onychorhynchus* as a member of the flatbill group, I recognize this conservativeness and at the same time acknowledge that convergence has occurred (as exhibited by *Myiobius,* for example) in the evolution of the tracheobronchial junction of the syrinx, the pendant, enclosed nest, the ossification of the interorbital septum, and the long, rictal bristles. A resolution of these conflicting views will require input from another character complex, perhaps using a biochemical approach.

The other case of the evolution of a basic configuration of the syrinx similar to that of *Rhynchocyclus* and *Tolmomyias* is in the *Phylloscartes* group in my *Elaenia* assemblage (Lanyon, 1988a). Four genera within this group build nests that are enclosed and with side entrance, and in addition have one A element complete around each bronchus and a calcified pessulus continuous with one of the other A elements; these are *Zimmerius, Phylloscartes, Mionectes,* and *Leptopogon.* The nests of *Zimmerius* and *Phylloscartes* are reported as being located within masses of vegetation such as moss or dead leaves, i.e., not pendant, while those of *Mionectes* and *Leptopogon* are usually suspended (as in the flatbills and *Onychorhynchus*) in a dark cleft or recess, often over water (Lanyon, 1988a). But the nasal septa in these genera are usually well ossified and have trabecular plates located within the septa (the characteristic feature of the entire *Elaenia* assemblage). External morphology also argues against regarding *Onychorhynchus* as a member of the *Phylloscartes* group; consequently, there has been no suggestion in the literature that *Onychorhynchus* might be closely related to *Mionectes* or *Leptopogon* (Hellmayr, 1927; Traylor, 1977).

Traylor (1977) cited suggestions by Wetmore (1972) and Eisenmann (in litt.) that *Onychorhynchus* might be most closely related to *Lophotriccus* because of similarities in egg color and crest display, but discounts these in the absence of support from Warter's (1965) cranial characters and Ames' (1971) syringeal characters. *Onychorhynchus* and *Lophotriccus* have very different basic configurations of the syrinx. The position taken here is that *Onychorhynchus* is a member of the flatbill group, which in turn is the sister-group to the tody-tyrants, of which *Lophotriccus* is a bona-fide member; but *Lophotriccus* is certainly closer to the other tody-tyrants than to *Onychorhynchus*.

Cnipodectes

Sclater (1888) expressed uncertainty about his placement of *Cnipodectes* between *Hirundinea* and *Myiobius* in his Tyranninae, and Berlepsch (1907) brought *Cnipodectes* into his Rhynchocyclinae. Since Berlepsch, it has been considered closely allied to the flatbills (Hellmayr, 1927; Warter, 1965; Traylor, 1977). Ames (1971) did not examine a syrinx of *Cnipodectes.*

I have examined two skulls of the monotypic *Cnipodectes* and agree with Warter (1965) that the nasal septum is basically like that of *Rhynchocyclus* and *Tolmomyias,* i.e., largely unossified (character 1), and the interorbital septum is like that found in all members of the assemblage except *Onychorhynchus* (character 2). The only report that I can find of the nest of *Cnipodectes* is Wetmore's (1972) quote from a letter from Alexander Skutch that describes one under construction as being pendant and enclosed, like that of others in this assemblage (character 3), but "nearly a meter" in length (character 14), recalling the unusual length of the nest of *Onychorhynchus*. The eggs are unknown.

The syrinx of *Cnipodectes* (six specimens examined; fig. 13: 7, 8) has no complete A ring around either bronchus (excluding the genus from the group consisting of *Rhynchocyclus* and its allies) and lacks the unique syringeal features that characterize the tody-tyrants (discussed below). For these reasons *Cnipodectes* occupies a singular position within the unresolved trichotomy illustrated in figure 1. The calcified pessulus is attached to the A4s. The internal cartilages are large and basically linear, as in *Rhynchocyclus,* but are forked distally and attached to the dorsal ends of the A3s (character 18). The B2 elements are slightly forked dorsally (character 19), a unique character state within the assemblage.

Zimmer (1939) has described a curious sexual dimorphism in this species, in which the male has the basal part of the shaft of the outer primaries arcuate and all of the primaries more or less twisted (character 20).

The Tody-tyrant Group

The small-bodied, relatively broad-billed birds known as the tody-tyrants include the smallest of the New World flycatchers, with proportionately long bills and tarsi. They have a long history of being grouped together in classifications, implying close relationship (Sclater, 1888; Berlepsch, 1907; Hellmayr, 1927; Zimmer, 1940, MS). The group is dominated numerically by *Hemitriccus* and *Todirostrum,* and in addition currently includes *Poecilotriccus, Myiornis, Lophotriccus, Atalotriccus,* and *Oncostoma* (Traylor, 1979; Traylor and Fitzpatrick, 1982).

The nasal septum in the tody-tyrants (examined in 30 of the 49 species, representing all genera) is poorly ossified and similar to that found in *Rhynchocyclus* and the other flatbills (character 1). Figures 4–7 illustrate the extent of intra- and intergeneric variation in the nasal capsule of the tody-tyrants. There is a remarkable uniformity in my series of tody-tyrant skulls with regard to the degree to which the infraorbital fenestra is enlarged and the supraorbital fenestra is obliterated (character 2). Figure 9 illustrates the intergeneric variation in this character within the tody-tyrants.

Nests are known for 18 of the 49 species of tody-tyrants, representing all of the genera, and all reported thus far are of the pendant, enclosed nest form, with side entrance (character 3).

I accept the overall similarity exhibited by the external morphology, foraging behavior, and vocal behavior of the tody-tyrants (Traylor and Fitzpatrick, 1982; Parker, 1982; Remsen et al., 1982) and these criteria can be useful in a general diagnosis of the group. None of these characters unequivocally demonstrates monophyly, however. For this purpose I call attention to what I perceive to be two uniquely derived syringeal characters. There is no complete A element around each of the bronchi, as found in the syrinx of the flatbills. There is a plate of weakly to moderately staining cartilage that interconnects the dorsal ends of the ossified A elements (half rings) in each bronchus and the ossified pessulus, thus forming a horseshoe-shaped or V-shaped structure that has its ventral edge within the internal tympaniform membranes and its apex at the tracheobronchial junction (character 21). This cartilaginous "horseshoe" is quite variable in size and width, as illustrated by some of the better stained examples labeled "C" in figures 14–16, but this variability seems to be correlated with species boundaries rather than generic limits. That Ames (1971) reported the "horseshoe" as present in some of the genera in his group of tody-tyrants but absent in others is explained by his not staining for cartilage. The structure is barely perceptible even in some of my stained specimens, but nevertheless is present in all of the species whose syringes are available.

The internal cartilages of tody-tyrants are delicate, slender, and inconspicuous rods located dorsally in the internal tympaniform membranes near the caudal ends of the "horseshoe" (character 22). Some appear to be barely attached to the "horseshoe" while others may have no apparent connection with that structure. Because of their fragile nature these cartilages are sometimes distorted or lost during dissection or subsequent handling; this fact, coupled with the lack of stained material, may explain Ames' (1971) failure to report internal cartilages for a number of genera in his tody-tyrant group. Their delicate nature and position with respect to the "horseshoe" make these cartilages unique among all tyrant flycatchers; they have been labeled "i" in those specimens in figures 14–16 in which they are most demonstrable.

After reviewing the anatomical studies by Warter (1965) and Ames (1971), Traylor (1977) commented: "Since this tody-tyrant group is uniform in cranial and syringeal characters, I doubt if further anatomical study will help clarify the relationships [within the group]." Unexpectedly, then, a comprehensive examination of syringeal morphology has revealed the need for recognizing new generic limits and for a realignment of a number of the species. The syrinx, in addition to providing the most reliable means of establishing monophyly for the assemblage, also furnishes clues for reevaluating evolutionary relationships within the assemblage. In this section I review the taxonomic treatment of these genera (table 2), reconstruct what I believe to be their evolutionary history (fig. 1), and make suggestions for a more appropriate taxonomy. To facilitate comparisons in table 2, taxa have been aligned horizontally insofar as possible, to correspond with the sequence and limits of genera recommended by this study (column on the right), hence the sequence of genera and species in the other columns is not necessarily that of those authors.

Most of the changes in the taxonomy of the tody-tyrants during this century have involved the merger of Hellmayr's 11 monotypic genera. Only two of these, *Oncostoma* and *Atalotriccus,* remain essentially as Hellmayr saw them (Traylor, 1977). Most workers since Hellmayr have merged *Perissotriccus* with *Myiornis. Colopteryx* was retained by Zimmer (MS) but merged with *Lophotriccus* by Traylor. Of the remaining seven monotypic genera recognized by Hellmayr, Zimmer retained six but greatly enlarged the concept of *Idioptilon* to include Hellmayr's polytypic *Euscarthmornis.* Fitzpatrick further enlarged *Idioptilon* to include *Snethlagea, Microcochlearius,* and *Ceratotriccus,* and Traylor continued this trend by also incorporating *Hemitriccus,* a name having priority over *Idioptilon.*

Generic separation of the two largest genera of tody-tyrants (*Todirostrum* and *Idioptilon/Hemitriccus*) has been questioned (Zimmer, MS; Meyer de Schauensee, 1966; Short, 1975), and a number of "intermediate species" (*plumbeiceps, russatum,* and *mirandae*) have been variously assigned to one or the other (table 2). Fitzpatrick (1976) and Traylor (1977) were reluctant to merge these genera, however.

When one examines a representative series of syringes of the tody-tyrants, a striking dichotomy is apparent at once. Among the sev-

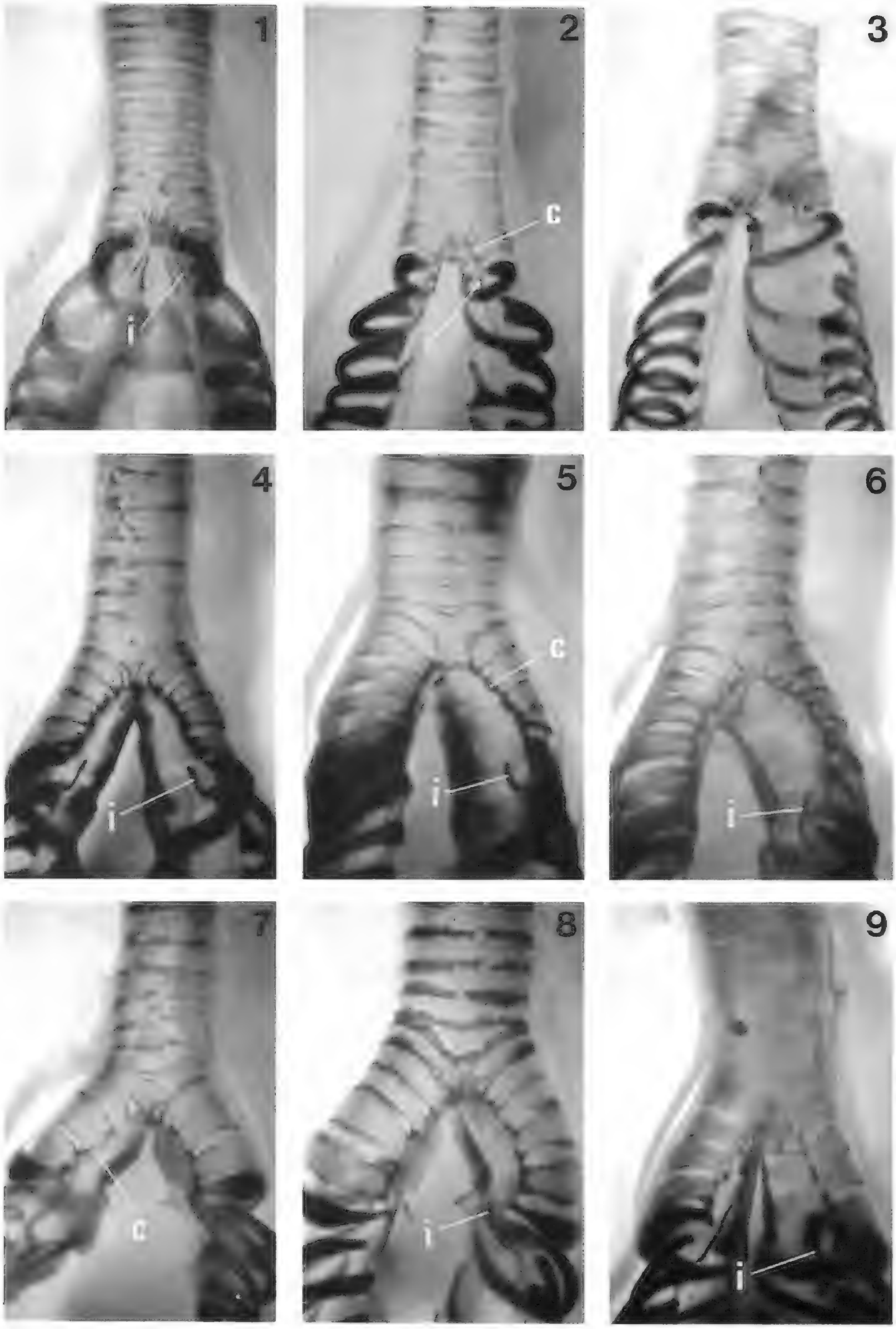

Fig. 14 The syringes of *Todirostrum* and *Poecilotriccus* (dorsal aspect; magnification = 12×): (**1**) *T. maculatum,* LSU 111086; (**2**) *T. cinereum,* AMNH 6810; (**3**) *T. chrysocrotaphum,* FMNH 291695; (**4**) *T. plumbeiceps,* PMNH 2812; (**5**) *T. sylvia,* PMNH 4823; (**6**) *T. latirostre,* AMNH 2295; (**7**) *Poecilotriccus capitale,* LSU 118052; (**8**) *P. albifacies,* FMNH 291693; (**9**) *P. ruficeps,* LSU 89490. **c** = cartilaginous "horseshoe" interconnecting the dorsal ends of the ossified A elements of each bronchus; **i** = internal cartilages.

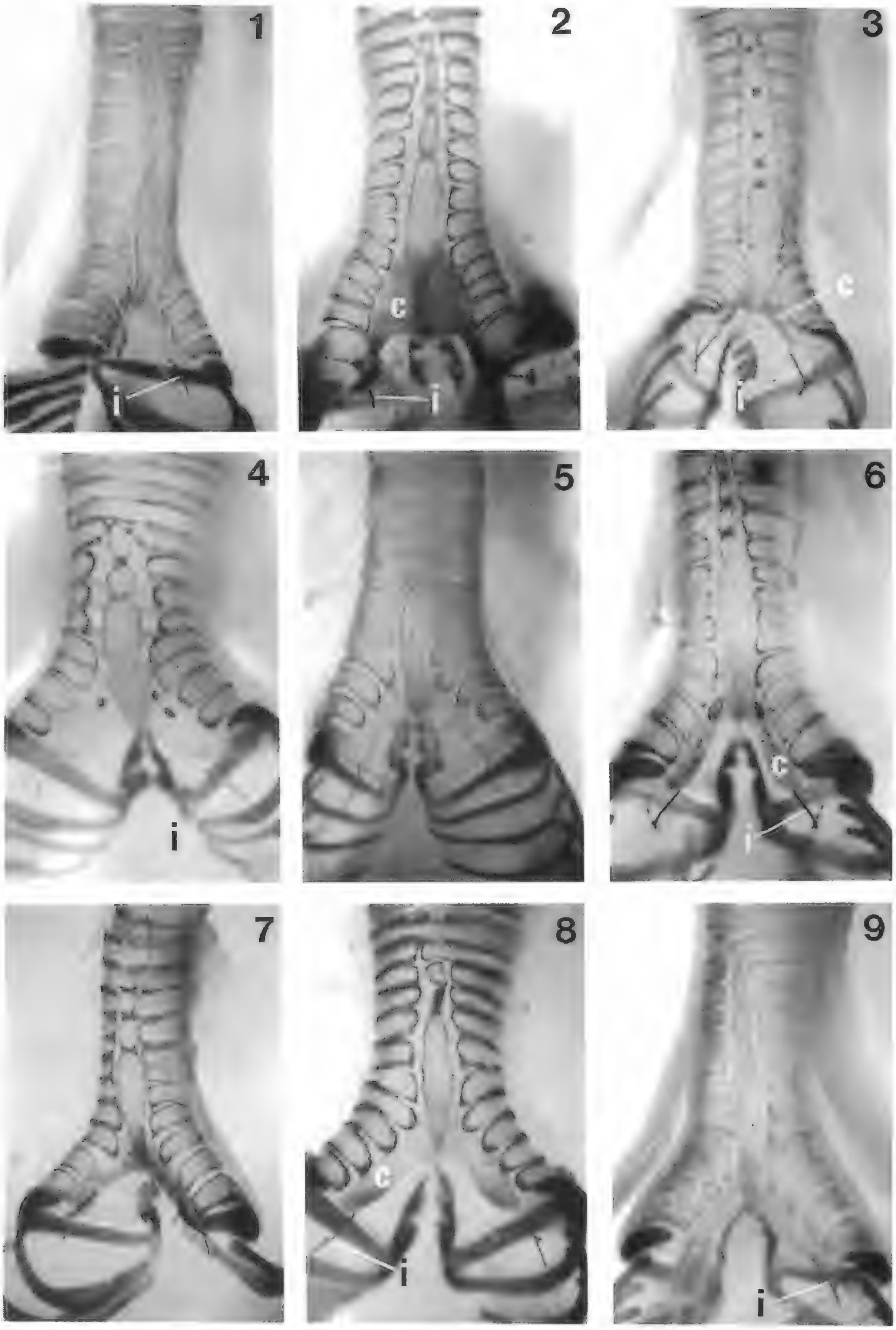

Fig. 15. Intrageneric variation in the syringes of nine species of *Hemitriccus* (dorsal aspect; magnification = 12×): (**1**) *diops*, PMNH 10744; (**2**) *flammulatus*, LSU 102637; (**3**) *granadensis*, LSU 107661; (**4**) *margaritaceiventer*, AMNH 2459; (**5**) *iohannis*, FMNH 323196; (**6**) *rufigularis*, FMNH 290386; (**7**) *zosterops*, LSU 102617; (**8**) *striaticollis*, LSU 79599; (**9**) *obsoletus*, USNM 503780. Labels as in figure 14.

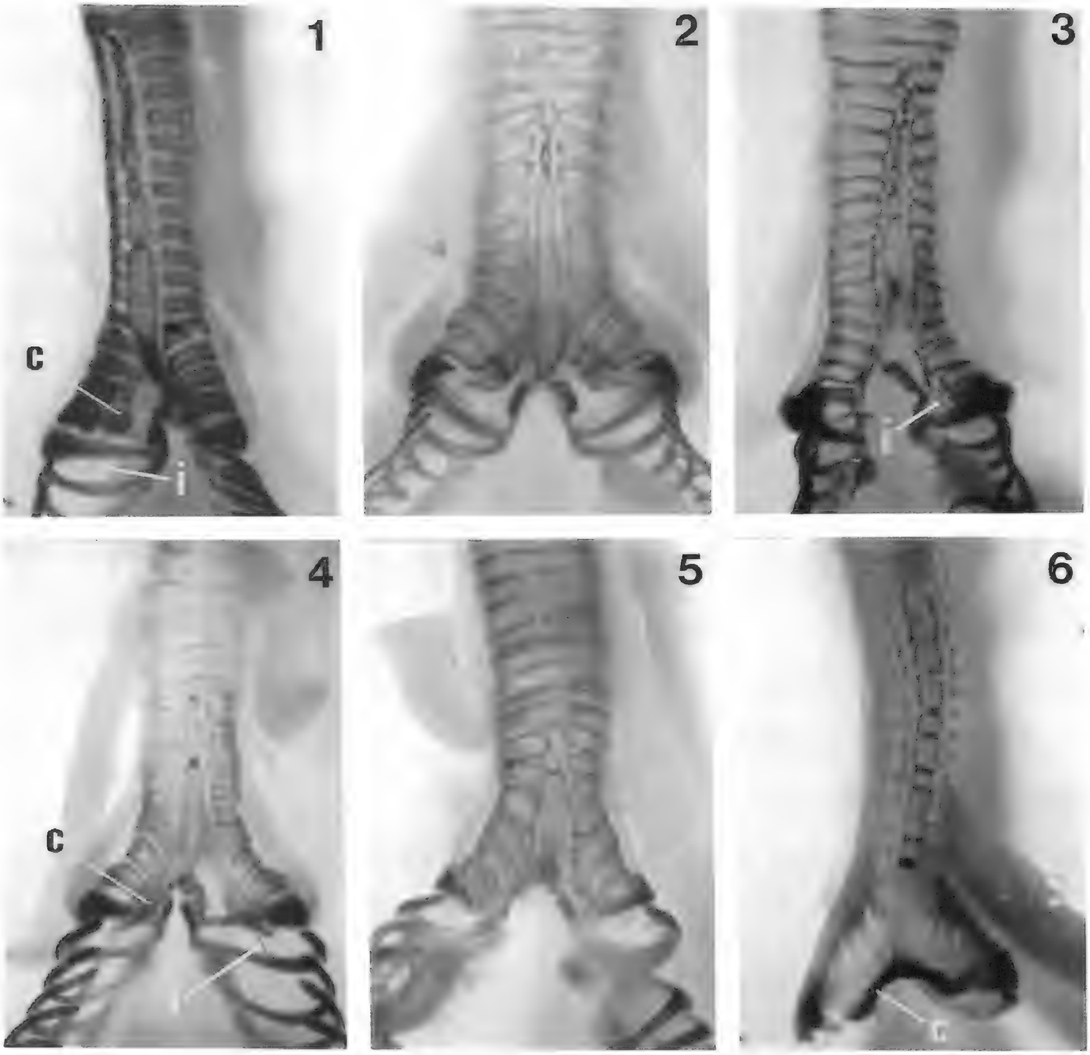

Fig. 16. The syringes of four genera among the tody-tyrants (dorsal aspect; magnification = 10× in 1–3, 13× in 4, 5, and 7× in 6): (**1**) *Lophotriccus galeatus,* AMNH 816783; (**2**) *L. pileatus,* PMNH 8931; (**3**) *Atalotriccus pilaris,* USNM 512583; (**4**) *Myiornis auricularis,* PMNH 2728; (**5**) *M. ecaudatus,* LSU 115987; (**6**) *Oncostoma olivaceum,* PMNH 7339. Labels as in figure 14.

eral structural groups of tyrant flycatchers that Ames (1971) considered to be distinguishable, "each with a high degree of syringeal homogeneity and with certain features not found elsewhere in the family," is his "*Colopteryx* group." He assigned six species (*Myiornis auricularis, Hemitriccus diops, Euscarthmornis* [*Hemitriccus*] *margaritaceiventer, Oncostoma cinereigulare, Lophotriccus pileatus,* and *Colopteryx* [*Lophotriccus*] *galeatus*) to this group, on the basis of "the long dorsal extension of the pessulus, accompanied by dorsally incomplete [A] elements." I agree with Ames and can add that 13 additional species from these 4 genera share this same derived character, as does *Atalotriccus pilaris* (figs. 15, 16). Ames also reported that his six species possessed "long, narrow, overlapping Mm. obliqui ventrales," not found in other flycatchers. This is more difficult for me to confirm in my cleared and stained specimens. Conspicuously absent from Ames'

"*Colopteryx* group" are the three species of *Todirostrum* for which he had syringes; he was unable to place that genus taxonomically. I suspect that the two syringeal characters by which I have established monophyly for the tody-tyrants as a whole (including *Todirostrum*) were not sufficiently evident for Ames to have attached any significance to them in his unstained specimens. I can confirm that the three species of *Todirostrum* examined by Ames do not have the character shared by the members of his "*Colopteryx* group," nor do the five other species in this genus available to me, or the five species currently in the genus *Poecilotriccus* (not examined by Ames). That the syringes of *Todirostrum* and *Poecilotriccus* have much in common will be discussed in detail below; on the basis of syringeal morphology both genera must be positioned outside of the cluster of five genera identifed above (*Myiornis, Hemitriccus, Lophotriccus, Atalotriccus,* and *Oncostoma*).

Todirostrum and *Poecilotriccus*

As part of the first meaningful analysis of evolution among the tody-tyrants, Fitzpatrick (1976) subdivided *Todirostrum* (table 2) into three groups: the "*cinereum* species group," the "*sylvia* species group," and the "aberrant" *capitale* with its remarkable sexual dimorphism and less spatulate-shaped bill. This suggestion of a close relationship between *capitale* and *Todirostrum* goes back at least to Sclater (1888), who also included *ruficeps* in *Todirostrum.* Ridgway (1907) excluded *ruficeps* from *Todirostrum* on account of its bushy crest and less spatulate-shaped bill and returned it to *Poecilotriccus*; he also noted that *capitale* (unseen by him) possibly should be referred to that genus as well. Nevertheless, most subsequent workers have retained *capitale* in *Todirostrum,* along with the closely allied but poorly known *tricolor* and *albifacies* (described much later, from very restricted ranges). Fitzpatrick (1976) acknowledged that the affinities of *capitale* might be closer to *Poecilotriccus ruficeps* and *Taeniotriccus andrei,* which he maintained as monotypic genera in the traditional manner. But, unlike previous workers, he placed these "relict species" immediately before *Todirostrum* in his sequence of genera, in recognition of a close relationship via *capitale.* Traylor (1977) argued correctly that retaining *capitale* within *Todirostrum* (while admitting closer ties with *ruficeps* and *andrei*) made that genus polyphyletic, and consequently he placed these three species in a single genus, for which *Poecilotriccus* is the oldest available name. Having removed *capitale* from *Todirostrum,* however, Traylor saw no particularly close relationship between *Todirostrum* and *Poecilotriccus* and separated them in his sequence of genera by *Hemitriccus* and *Oncostoma,* following the tradition of Berlepsch (1907), Hellmayr (1927), and Zimmer (MS).

I was able to examine the syringes of 8 of the 14 species of *Todirostrum,* as recognized by Traylor (1979) (*nigriceps, pictum, viridanum, fumifrons, russatum,* and *senex* lacking) and found that there are two very distinct types of syrinx within this sample. This division of my sample based on syringeal morphology is concordant with Fitzpatrick's (1976) recognition of two major species groups on the basis of plumage color and pattern (table 2), with the exception of *calopterum* as discussed below.

The least specialized syrinx among the tody-tyrants is that found in my eight specimens of *Todirostrum cinereum, T. chrysocrotaphum, T. poliocephalum,* and *T. maculatum* (fig. 14: 1–3), each of which is a representative of Fitzpatrick's *cinereum* species group. Usually there are but two calcified half-rings (A1 and A2) supporting each bronchus, though two specimens had incomplete A3 elements located caudal to the tracheobronchial junction as well. The calcified pessulus typically is continuous dorsally and ventrally with the complete A4 element (i.e., only A1 through A3 are incomplete), though in one specimen the A4 element is incomplete dorsally and the pessulus is fused with the complete A5 element. The overall impression is of a comparatively simple syrinx, with little specialization in each bronchus except for the characters 21 and 22 that unite all tody-tyrants.

My nine specimens of *Todirostrum sylvia, T. latirostre, T. plumbeiceps,* and *T. calopterum* all representatives of Fitzpatrick's *sylvia* species group except for *calopterum,* are readily separable from those of the *cinereum* species group by virtue of their having four or five incomplete A elements in each bron-

Table 2
Comparison of Classifications of the Tody-tyrants

Hellmayr (1927)	Zimmer (MS, ca. 1955)	Fitzpatrick (1976)	Traylor (1977, 1979)	This study
TODIROSTRUM	TODIROSTRUM	TODIROSTRUM	TODIROSTRUM	TODIROSTRUM
		"*cinereum* group"		
chrysocrotaphum	*chrysocrotaphum*[a]	*chrysocrotaphum*	*chrysocrotaphum*	*chrysocrotaphum*
nigriceps		*nigriceps*	*nigriceps*	*nigriceps*
pictum		*pictum*	*pictum*	*pictum*
cinereum	*cinereum*[b]	*cinereum*[b]	*cinereum*	*cinereum*
viridanum			*viridanum*	*viridanum*
poliocephalum	*poliocephalum*	*poliocephalum*	*poliocephalum*	*poliocephalum*
maculatum	*maculatum*	*maculatum*	*maculatum*	*maculatum*
calopterum	*calopterum*	*calopterum*	*calopterum*	POECILOTRICCUS
		"*sylvia* group"		*calopterum*
sylvia	*sylvia*	*sylvia*	*sylvia*	*sylvia*
latirostre	*latirostre*	*latirostre*	*latirostre*	*latirostre*
fumifrons	*fumifrons*	*fumifrons*	*fumifrons*	*fumifrons*
	plumbeiceps	*plumbeiceps*	*plumbeiceps*	*plumbeiceps*
	russatum	*russatum*	*russatum*	*russatum*
senex	*senex*	*senex*	*senex*	*senex*
mirandae[c]			POECILOTRICCUS	
capitale	*capitale*[d]	*capitale*[e]	*capitale*	*capitale*
POECILOTRICCUS	POECILOTRICCUS	POECILOTRICCUS		
ruficeps	*ruficeps*	*ruficeps*	*ruficeps*	*ruficeps*
			tricolor[f]	*tricolor*
TAENIOTRICCUS	TAENIOTRICCUS	TAENIOTRICCUS		*albifacies*
andrei	*andrei*	*andrei*	*andrei*	*andrei*
MYIORNIS	MYIORNIS	(not included in study)	MYIORNIS	HEMITRICCUS
auricularis	*auricularis*		*auricularis*	*auricularis*
albiventris	*albiventris*		*albiventris*	*albiventris*

Table 2—(*Continued*)

Hellmayr (1927)	Zimmer (MS, ca. 1955)	Fitzpatrick (1976)	Traylor (1977, 1979)	This study
PERISSOTRICCUS				
ecaudatus	*ecaudatus*		*ecaudatus*	*ecaudatus*
HEMITRICCUS	HEMITRICCUS	(not included in study)	HEMITRICCUS	
diops[g]	*diops*		*diops*	*diops*
	obsoletus		*obsoletus*	*obsoletus*
	flammulatus	IDIOPTILON	*flammulatus*	*flammulatus*
CERATOTRICCUS	CERATOTRICCUS	“*brown* group”		
furcatus	*furcatus*	*furcatum*	*furcatus*	*furcatus*
IDIOPTILON	IDIOPTILON			
rothschildi[h]				
EUSCARTHMORNIS				
granadensis	*granadense*	*granadense*	*granadensis*	*granadensis*
	mirandae[i]	*mirandae*	*mirandae*	*mirandae*
plumbeiceps[j]		*kaempferi*	*kaempferi*	*kaempferi*
russatus[j]				
rufigularis	*rufigulare*	*rufigulare*	*rufigularis*	*rufigularis*
		“*green* group”		
	zosterops	*zosterops*	*zosterops*	*zosterops*
	aenigma[k]	*aenigma*	*aenigma*	*aenigma*
orbitatus	*orbitatum*	*orbitatum*	*orbitatus*	*orbitatus*
striaticollis[l]	*striaticolle*	*striaticolle*	*striaticollis*	*striaticollis*
			iohannis[m]	*iohannis*[m]
nidipendulus	*nidipendulum*	*nidipendulum*	*nidipendulus*	*nidipendulus*
spodiops	*spodiops*	*spodiops*	*spodiops*	*spodiops*
margaritaceiventer	*margaritaceiventer*	*margaritaceiventer*	*margaritaceiventer*	*margaritaceiventer*
inornatus	*inornatum*	*inornatum*	*inornatus*	*inornatus*
SNETHLAGEA	SNETHLAGEA			*cinnamomeipectus*[n]
minor	*minor*	*minor*	*minor*	*minor*
MICROCOCHLEARIUS	MICROCOCHLEARIUS			
josephinae	*josephinae*	*josephinae*	*josephinae*	*josephinae*
LOPHOTRICCUS	LOPHOTRICCUS	(not included in study)	LOPHOTRICCUS	LOPHOTRICCUS
pileatus	*pileatus*		*pileatus*	*pileatus*
vitiosus[o]	*vitiosus*		*vitiosus*	*vitiosus*
	eulophotes		*eulophotes*	*eulophotes*

Table 2—(*Continued*)

Hellmayr (1927)	Zimmer (MS, ca. 1955)	Fitzpatrick (1976)	Traylor (1977, 1979)	This study
COLOPTERYX	*colopteryx*	(not included in study)		
galeatus	*galeatus*		*galeatus*	*galeatus*
ATALOTRICCUS	ATALOTRICCUS	(not included in study)	ATALOTRICCUS	
pilaris	*pilaris*		*pilaris*	*pilaris*
ONCOSTOMA	ONCOSTOMA	ONCOSTOMA	ONCOSTOMA	ONCOSTOMA
cinereigulare[p]	*cinereigulare*[p]	*cinereigulare*[p]	*cinereigulare*	*cinereigulare*
			olivaceum	*olivaceum*

[a] Includes *nigriceps* and *pictum* as subspecies.

[b] Includes *viridanum.*

[c] Placed in *Idioptilon* by Zimmer and Fitzpatrick, and in *Hemitriccus* by Traylor.

[d] Includes *tricolor,* described in 1946.

[e] Includes *tricolor* and *albifacies,* described in 1959.

[f] Includes *albifacies,* given specific status by Traylor and Fitzpatrick (1982).

[g] Includes *obsoletus* and *flammulatus* as subspecies.

[h] Synonymized by subsequent workers with a subspecies of *zosterops.*

[i] Included *kaempferi,* described as a subspecies in 1953.

[j] Placed in *Todirostrum* by subsequent workers.

[k] Described in 1940.

[l] Includes *zosterops,* given specific status by subsequent workers.

[m] Considered a subspecies of *striaticollis* by previous workers.

[n] Described in 1979.

[o] Includes *eulophotes.*

[p] Includes *olivaceum.*

chus caudal to the tracheobronchial junction, and these A elements are noticeably wider than their homologs in the *cinereum* group, thereby adding to the overall impression of a much longer bronchial component to the syrinx (fig. 14: 4–6). Not only is the bronchial component longer in these species, it is bowed or arched laterally so that the cartilaginous plate interconnecting the dorsal ends of the bronchial A1 half-rings (character 21) is truly horseshoe-shaped rather than V-shaped as in the *cinereum* species group. These features contributing to an enlarged bronchial component of the syrinx undoubtedly are interrelated, and I refer to them collectively as character 23. Additionally, *sylvia* and its near relatives have a greatly enlarged and very conspicuous plate of cartilage connecting the ventral ends of the A1 through A4 elements and extending well into the internal tympaniform membrane (character 24). This plate is present but much less developed and noticeable in the *cinereum* group.

The similarity between the syringes of my two specimens of *calopterum* and those of the species within the *sylvia* group is unexpected in view of the fact that Fitzpatrick had placed *calopterum* within his *cinereum* group. This is the only departure from Fitzpatrick's division of *Todirostrum* that is indicated by syringeal morphology, bearing in mind that syringes are still unavailable for 6 of the 14 species. The relationship of *calopterum* merits close scrutiny with a biochemical approach.

Quite unexpectedly (Ames did not have access to *Poecilotriccus*) I discovered that my nine syringes of the five species of *Poecilotriccus* (as recognized by Traylor and Fitzpatrick, 1982) are like those of the three species representing the *sylvia* group in *Todirostrum,* for they too possess characters 23 and 24. My single syrinx of *andrei* is somewhat intermediate in that there are only three incomplete A elements in each bronchus (instead of four or five), but these half-rings are much wider than those in the syringes of the *cinereum* species group of *Todirostrum,* preserving the aspect of the longer, bowed bronchial component characteristic of *Poecilotriccus* (character 23). Syringes of three species of *Poecilotriccus* are illustrated in figure 14: 7–9 and should be compared with syringes of the *sylvia* group in figure 14: 4–6.

Even after eliminating the species (*ruficeps*) referred to *Poecilotriccus,* Ridgway (1907) noted that the genus *Todirostrum* "is still a heterogeneous one, and probably will require further subdivision." Hellmayr (1927) commented on *Todirostrum*: "The genus, as circumscribed here [see table 2], is rather heterogeneous and probably requires subdivision, its members being exceedingly variable in shape of bill and color pattern." However, it is not clear whether Hellmayr intended these remarks to go beyond the two species that were obviously different: (1) *mirandae,* which all subsequent authors have placed in either *Idioptilon* or *Hemitriccus* (a move supported by syringeal morphology; see below), and (2) *capitale.* That *sylvia* and its closest allies in *Todirostrum* are more closely related to *Poecilotriccus* than to the *cinereum* species group in *Todirostrum,* as revealed by syringeal morphology, has not been suggested in the literature previously.

The similarity in the syringes of the *sylvia* group and *Poecilotriccus* is reinforced by an external morphological character that these taxa share, namely the presence of rufous or cinnamon in the plumage of various regions of the head (character 25). If we are to assume that the ancestral stock of this branch of the tody-tyrant lineage possessed some degree of rufous about the head, then the character has been lost or greatly reduced in *fumifrons, calopterum,* and *sylvia,* but is well developed in *latirostre, russatum, plumbeiceps, capitale, ruficeps,* and *andrei.* No member of the *cinereum* group of *Todirostrum* has even a suggestion of rufous or cinnamon color; as Fitzpatrick (1976) has indicated, their colors are predominantly yellow, green, black, or dark gray.

The differences between the syringeal morphology of the two major species groups in *Todirostrum* exceed the limits of intrageneric variation within the family Tyrannidae, and the two groups should be given separate generic status. Since the type of *Todirostrum* (Lesson, 1831) is *cinereum,* the *cinereum* group of species retains that generic name (table 2). *Poecilotriccus* could be maintained generically distinct from the *sylvia* species group, following tradition in emphasizing differences in external morphology; this would require the determination of an available name or perhaps a new name for the *sylvia* group. In recognition of the conservative nature of syringeal morphology and the relative plasticity of plumage color and pattern among tyrant flycatchers, I recommend that the *sylvia* species group, formerly in *Todirostrum,* be merged with *Poecilotriccus* Berlepsch, 1884, the oldest available name for this enlarged genus (table 2). I am confident that this hypothesis will be supported by the results of a biochemical approach, possibly the only other approach with potential for revealing meaningful information on this unexpected relationship.

Hemitriccus, Lophotriccus, and *Oncostoma*

The remaining five genera (*Myiornis, Hemitriccus, Lophotriccus, Atalotriccus,* and *Oncostoma*) currently recognized in this assemblage (Traylor, 1979) have a derived syringeal character found in no other suboscines, as noted above and reported by Ames (1971): the calcified pessulus extends anteriorly to divide a number of the A elements dorsally (character 26) (figs. 15, 16). Because of the complexity and uniqueness of this derived character, it is difficult not to regard these five genera as a monophyletic group within the tody-tyrant assemblage. Unfortunately, neither syringeal morphology nor external morphology is unequivocally useful in determining relationships between *Todirostrum, Poecilotriccus,* and the lineage containing the remaining genera in the assemblage (i.e., those possessing character 26), hence the unresolved trichotomy in figure 1. Here again, a biochemical approach may prove helpful.

The taxonomic history of the taxa that Traylor (1979) assigned to *Myiornis* and *Hemitriccus* is a complicated one (see table 2). In addition to two species of *Myiornis* and his core genus *Euscarthmornis,* Hellmayr (1927) recognized no less than six monotypic genera, differentiated by peculiarities of the tail (*Perissotriccus* and *Ceratotriccus*), wing (Idioptilon), tail and wing (*Hemitriccus*), tail and bill (*Microcochlearius*), and bill and nostrils (*Snethlagea*). Subsequent authors attached less significance to these differences in shape and size. Zimmer (1940) wrote: "I believe that the short tail of '*Perissotriccus*' is not a sufficient character in itself to warrant the recognition of this group as a genus distinct from *Myiornis.*" Of *Microcochlearius* Zimmer (MS) commented: "Doubtfully distinct from *Idioptilon,*" the genus he used to incorporate Hellmayr's *Euscarthmornis.* Fitzpatrick (1976) likewise used this enlarged concept of *Idioptilon,* which he subdivided into a "brown plumaged group" and a "green plumaged group"; he merged *Ceratotriccus* into the former, on the basis of shared morphologic similarities and biogeographic considerations, and *Microcochlearius* and *Snethlagea* into the latter. Traylor (1977) accepted all of the above changes, but he considered *Hemitriccus* to belong to the green species group in *Idioptilon,* necessitating the use of the older name, *Hemitriccus,* for the enlarged genus. Though he reduced this particular complex of taxa to but two genera, *Myiornis* and *Hemitriccus*, Traylor (1977) did not regard these genera as sister taxa. His sequence for the group (not evident from the arrangement of convenience in table 2) was *Myiornis, Lophotriccus, Atalotriccus, Oncostoma,* and *Hemitriccus,* in the tradition of most earlier workers.

The least specialized syrinx among the taxa possessing character 26 is that found in Traylor's (1979) *Myiornis* and *Hemitriccus.* The syringes of these taxa are remarkably similar, varying only in the number of A elements that are divided dorsally by the pessulus (from 4 to 14). The syringes of *Myiornis* (6 specimens of 2 species examined; *albiventris* lacking) average fewer divided A elements (fig. 16: 4, 5) than do those of *Hemitriccus* (22 specimens of 11 species examined; *josephinae, aenigma, spodiops, orbitatus, inornatus, mirandae, kaempferi, cinnamomeipectus,* and *furcatus* lacking) as illustrated in figure 15. However, I cannot place some specimens with certainty in one or the other of these genera. Nor am I able to distinguish between Fitzpatrick's (1976) "brown" and "green" groups within his *Idioptilon* on the basis of syringeal morphology. This is not an argument against such an intrageneric subdivision, but merely a reflection of the conservative nature of the syrinx and its inadequacy for resolving interrelationships at that level. Because of this great similarity of the syrinx and the lack of significant differentiation in external morphology, I recommend that *Myiornis* be merged with *Hemitriccus,* creating a single genus of 23 species, a relationship not heretofore suggested in the literature.

Hellmayr (1927) questioned the wisdom of separating *Lophotriccus* and *Colopteryx,* the only tody-tyrants with distinctive crests, and Traylor (1977) merged them with the remark that he does "not consider peculiar primaries a 'generic' character in the flycatchers." Workers prior to Hellmayr (1927) often merged *Atalotriccus pilaris* with *Colopteryx,* but subsequent authors generally have recognized this monotypic genus because of its extreme reduction in size of the outer primaries (Traylor and Fitzpatrick, 1982). Traylor (1977) noted that "*Atalotriccus* has been kept with *Colopteryx* because both have shortened outer primaries. If *Atalotriccus* has indeed been derived from *C. galeatus,* then the ornamental crest must have been lost secondarily. But it is just as easy to conceive *Atalotriccus* as an *Idioptilon* that has independently acquired reduced outer primaries and converged on *Colopteryx* in this character. The relatively long *Atalotriccus* tarsus is more like that of *Idioptilon* than that of *Lophotriccus.* Eisenmann (in litt.) believes *Atalotriccus* behaves more like *Todirostrum sylvia* than like *Lophotriccus.* Considering the doubts about the origin of *Atalotriccus,* I accept it as a distinct genus."

Oncostoma traditionally has been considered more closely related to the *Idioptilon/Hemitriccus* group than to either *Lophotriccus* or *Atalotriccus* (Hellmayr, 1927; Zimmer, MS). Fitzpatrick (1976) noted that "*Oncostoma*—the Bentbill—represents a rather divergent Central American offshoot from *Idioptilon,* and its generic separation appears to be warranted"; he omitted *Lophotriccus* and *Atalotriccus* from his study of the tody-tyrants. Traylor and Fitzpatrick (1982), in discussing the merger of several monotypic genera (having oddly shaped bills and tails) with *Hemitriccus,* suggested that *Oncostoma* probably "should join the throng as the only Central American representative; its sole peculiarity, besides an odd voice, is mentioned in its English name."

The three genera (*Lophotriccus, Atalotriccus,* and *Oncostoma*) have a syrinx like that of *Hemitriccus,* in that it possesses character 26, but this syrinx differs with respect to a derived character not found elsewhere in the Tyrannidae. The tracheobronchial junction, and indeed the entire trachea, has undergone a conspicuous compression laterally; consequently the syrinx is quite narrow when viewed from the dorsal aspect (as in all of the accompanying figures) and unusually broad when viewed from the lateral aspect (character 27) (fig. 16: 1–3, 6).

The only variation in syringeal morphology among these taxa (*Lophotriccus, Atalotriccus,* and *Oncostoma*) is in the number of A elements that are divided dorsally by the pessulus. My 2 specimens of *Atalotriccus pilaris* (fig. 16: 3) and 10 specimens of the 4 species of *Lophotriccus* (including *Colopteryx*; fig. 16: 1, 2) have from 10 to 18 divided A elements; the syringes of these genera are not distinguishable. Given the evolutionary alternatives of an *Atalotriccus* having lost its ornamental crest secondarily (i.e., a common origin with *Lophotriccus*) or having evolved independently a syrinx and reduced outer primaries like those of *Lophotriccus* (i.e., a closer affinity with *Idioptilon/Hemitriccus*), the former is more parsimonious; I recommend that *Atalotriccus* be merged with *Lophotriccus.*

My seven specimens of the two species of *Oncostoma* have from 19 to 23 divided A elements (character 28) (fig. 16: 6), making this syrinx the most highly specialized of all the tody-tyrants. For the present I maintain *Oncostoma* in a distinct genus, on the basis of syringeal morphology and the unique shape of the bill, though if a biochemical approach were to discern no greater genetic difference between *Oncostoma* and *Lophotriccus* than between *Atalotriccus* and *Lophotriccus,* I would support a merger of all three into *Oncostoma,* the oldest available name.

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APPENDIX

List of anatomical specimens (121 skulls, 130 syringes) examined for developing a phylogeny of the flatbills and tody-tyrants. Genera and species, including putative relatives, are listed alphabetically. All known species within the assemblage are given, including those for which specimens are lacking. Not included here are the species in over 100 other genera of tyrant flycatchers whose skulls and syringes have been examined for outgroup comparison.

	Skulls	Syringes
Atalotriccus pilaris. See *Lophotriccus pilaris*		
Caenotriccus spp. See *Pseudotriccus* spp.		
Ceratotriccus furcatus. See *Hemitriccus furcatus*		
Cnipodectes subbrunneus	AMNH 14159; USNM 347798	LSU 115934, 108464, 108465, 110701, 110702; PMNH 6678
Colopteryx galeatus. See *Lophotriccus galeatus*		
Corythopis delalandi	AMNH 14476; UMMZ 159072, 202249	Lacking
C. torquata	AMNH 14164; FMNH 290301	AMNH 8963, 816755; LSU 101549, 102782
Hemitriccus aenigma	Lacking	Lacking
H. albiventris	LSU 101516	Lacking
H. auricularis	UMMZ 158811	LSU 102622; PMNH 2726, 2728
H. cinnamomeipectus	LSU 84043	Lacking
H. diops	UMMZ 200865	PMNH 10743, 10744
H. ecaudatus	LSU 73120	LSU 108505, 108506, 115987
H. flammulatus	AMNH 14162; FMNH 323186; LSU 94080	LSU 102635, 102637
H. furcatus	Lacking	Lacking
H. granadensis	AMNH 14161; LSU 70249	LSU 107661
H. inornatus	Lacking	Lacking
H. iohannis	FMNH 315968	FMNH 323195, 323196
H. josephinae	Lacking	Lacking
H. kaempferi	Lacking	Lacking
H. margaritaceiventer	DMNH 68129; UMMZ 200862, 200863; USNM 346038	AMNH 2459, 6783
H. minor	USNM 346033	FMNH 330594; MG A5026
H. mirandae	Lacking	Lacking
H. nidipendulus	Lacking	FMNH 107239, 107241, 107243
H. obsoletus	Lacking	USNM 503780
H. orbitatus	Lacking	Lacking
H. rufigularis	FMNH 315972; LSU 107316	FMNH 290386; LSU 107662
H. spodiops	Lacking	Lacking
H. striaticollis	LSU 86572	LSU 79599, 105211
H. zosterops	FMNH 323189; LSU 101513, 118272	AMNH 816784; LSU 102617, 102619
Idioptilon spp. See *Hemitriccus* spp.		

	Skulls	Syringes
Lophotriccus eulophotes	LSU 131692–131694	LSU 133549, 133550
L. galeatus	AMNH 15080, 15216, 15217; UMMZ 154738; USNM 344212, 344213	AMNH 9406, 9407, 816783
L. pilaris	AMNH 9034	CMNH 374; USNM 512583
L. pileatus	AMNH 14160; FMNH 323179; USNM 428688	LSU 108503; PMNH 8931
L. vitiosus	LSU 64861, 111580	LSU 71358, 118514, 120185
Microcochlearius josephinae. See *Hemitriccus josephinae*		
Myiornis spp. See *Hemitriccus* spp.		
Oncostoma cinereigulare	AMNH 11707, 12749, 12750; USNM 288853	AMNH 8230; CMNH 915; PMNH 2139
O. olivaceum	Lacking	LSU 108500, 108501; PMNH 7198, 7339
Onychorhynchus coronatus	AMNH 14163, 15210, 15211; FMNH 290294, 290295; LSU 50817; USNM 288900	AMNH 8781; LSU 102588, 110697, 115912
Perissotriccus ecaudatus. See *Hemitriccus ecaudatus*		
Platyrinchus cancrominus	UMMZ 153251	AMNH 6729
P. coronatus	AMNH 15212, 15213; UMMZ 153250, 214050	AMNH 8231; LSU 102599; MPEG 2238
P. flavigularis	Lacking	Lacking
P. leucoryphus	UMMZ 200851	Lacking
P. mystaceus	AMNH 6730, 7865, 7866; FMNH 291889–291892, 291900, 323235	AMNH 2461, 9865; PMNH 2758
P. platyrhynchos	FMNH 323240; LSU 101503	FMNH 330618; LSU 102593; MPEG 3533
P. saturatus	LSU 100949	AMNH 9398; FMNH 330610
Poecilotriccus albifacies	FMNH 323180	FMNH 291693
P. andrei	Lacking	USNM 562371
P. calopterus	FMNH 291887; LSU 111579	FMNH 323203; UMMZ 225033
P. capitale	LSU 118270	LSU 118052, 120184
P. fumifrons	Lacking	Lacking
P. latirostre	AMNH 6935; FMNH 290292	AMNH 2295, 3522; LSU 102612
P. plumbeiceps	UMMZ 200857	PMNH 2805, 2812
P. ruficeps	LSU 90056, 90057	LSU 89490
P. russatus	Lacking	Lacking
P. senex	Lacking	Lacking
P. sylvia	LSU 50820	PMNH 4823, 7212
P. tricolor	Lacking	FMNH 334373, 334375
Pseudotriccus pelzelni	LSU 86573	AMNH 8714; UK 69000, 69001
P. ruficeps	AMNH 6936, 6937, 6938	AMNH 3524; LSU 102626, 102627

	Skulls	Syringes
P. simplex	FMNH 323152; LSU 99426	FMNH 323153; LSU 98046
Ramphotrigon fuscicauda	FMNH 290293; LSU 101509–101511	LSU 102603, 102604, 102608
R. megacephala	LSU 101512	FMNH 291696; LSU 102610
R. ruficauda	LSU 62765, 86571	LSU 110718, 115966
Rhynchocyclus brevirostris	AMNH 14478	AMNH 4163, 6719; LSU 108488
R. fulvipectus	LSU 107315	FMNH 323210; LSU 89487
R. olivaceus	FMNH 315975; LSU 91260, 118512; USNM 344196, 347154	LSU 108485; PMNH 7343
Snethlagea minor. See *Hemitriccus minor*		
Taeniotriccus andrei. See *Poecilotriccus andrei*		
Todirostrum calopterum. See *Poecilotriccus calopterus*		
T. capitale. See *Poecilotriccus capitale*		
T. chrysocrotaphum	UMMZ 200608	FMNH 291695
T. cinereum	AMNH 7182, 12073	AMNH 6810; LSU 75471; UK 54770
T. fumifrons. See *Poecilotriccus fumifrons*		
T. latirostre. See *Poecilotriccus latirostre*		
T. maculatum	LSU 73212, 111582	FMNH 106092; LSU 111086
T. mirandae. See *Hemitriccus mirandae*		
T. nigriceps	UMMZ 153255	Lacking
T. pictum	Lacking	Lacking
T. plumbeiceps. See *Poecilotriccus plumbeiceps*		
T. poliocephalum	Lacking	FMNH 107001, 107002
T. russatum. See *Poecilotriccus russatus*		
T. senex. See *Poecilotriccus senex*		
T. sylvia. See *Poecilotriccus sylvia*		
T. viridanum	Lacking	Lacking
Tolmomyias assimilis	AMNH 15214, 15215; FMNH 323215; LSU 101506	AMNH 15214; LSU 71473, 102602
T. flaviventris	AMNH 9138, 12075; FMNH 323222	CMNH 1263; LSU 101508; USNM 318719
T. poliocephalus	FMNH 315990; LSU 70248	FMNH 290389; LSU 75570
T. sulphurescens	AMNH 10023, 10307, 12985	AMNH 4153, 6814, 8225

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